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Symposium: The Biogeography of Baja California and Adjacent Seas

PART II. MARINE BIOTAS

A Review of the Ecology, Distribution, and Affinities of the Benthic Flora

E. Y. DAWSON

ONLY 65 years have passed since the first investigations were made on the marine vegetation of Baja California, and these were neither by Mexican nor American workers, but by the French writer Hariot (1895) whose report on a few calcareous red algae was made in connection with studies of the former pearl oyster fisheries in the vicinity of La Paz. A few species of fleshy algae from the Gulf of California were reported by Howe (1911), but it was not until the expedition of the California Academy of Sciences to the Gulf of California in 1921 that any appreciable number of marine plants were collected from this region. On that trip, Ivan Johnston, a youthful phanerogamic botanist and student of W. A. Setchell at the University of California, was encouraged by his professor to make extensive collections of marine algae. This he did with uncommon ability, and he returned with over a hundred species which constituted the main material for a richly illustrated report by Setchell and Gardner (1924).

No collections had yet come from the Pacific Coast of Baja California or its islands, and it was again an expedition from the California Academy of Sciences which first brought home representations of these floras. The marine algae of Guadalupe Island and of the outlying Revillagigedo Archipelago became known first as the result of collections made by another associate of Setchell, H. L. Mason (Setchell and Gardner, 1930), and finally a few species were reported from the Pacific mainland coast of Baja California from still another California Academy expedition (Setchell and Gardner, 1932). It was not, however, until W. R. Taylor accompanied the Hancock expeditions of 1934 and 1939 to the Galápagos Islands that a trained algologist visited any part of the Baja California area. He added a number of species to the known floras of Pacific Baja California (Taylor, 1945) and led to a further interest in marine botany on the part of the Hancock Foundation. This resulted in the writer's participation in 1940 in the Hancock Expedition to the Gulf of California. Since 1940, the writer has been almost the sole investigator of the marine algae of this region. During this time, some 20 major collecting trips

have been made into the area, and nearly 50,000 specimens of marine algae prepared. This does not mean, however, that the region is as yet well known. The study of some groups has progressed well, and a taxonomic treatment of the red algae of Pacific Mexico is now more than half complete (Dawson, 1950d, 1953a, 1953b, 1954b). Studies are now in progress on the crustose members of the family Corallinaceae, and a treatment of the order Gigartinales is expected to be completed during the coming year. A total of nearly 700 species is now recorded from Baja California and its adjacent island and sea areas. Among these, 357 are known from Pacific Baja California, 329 from the Gulf of California, 90 from Guadalupe Island, 27 from Alijos Rocks, and about 90 from the Revillagigedo Archipelago. Much of the work since 1940, however, has been concerned with the ecology of the algae of this interesting Baja California region, and since this bears heavily upon marine zoological problems, it seems appropriate to consider here briefly the unique combination of environmental influences which provide for the remarkable diversity of benthic algal forms within this relatively small region of the eastern Pacific.

Baja California and the Gulf of California, with their triple coastline, extensive latitudinal range, and varied weather patterns, embrace as diversified a marine environment as almost any region of similar area in the world. Some of the outstanding features within the extreme range of ecological conditions will be taken up in turn before commenting upon the floral compositions of major areas.

When the writer first began to study the algae of northwestern Baja California, he did so after having become acquainted with the flora of the region of La Jolla, California, as a southern expression of the flora of the region of southern California south of Point Conception. It had long been known that Point Conception marked the southern limits of a number of species representing the cold water flora to the north which reaches its best development in the area of the Monterey Peninsula. At La Jolla, a similarly, richly diversified flora obtains in which a number of subtropical elements occur in keeping with progressively more southerly latitudes. A student of the marine flora of mainland southern California is, thus, impressed by the generally increasing prevalence of warm water elements between western Santa Barbara County and La Jolla, and, if he looks at this apart from certain basic hydrographic circumstances, he might assume that the trend to increasing prevalence of warm water forms would continue southward with decreasing latitude. In 1944, the algal flora of northwestern Baja California was virtually unknown, and, thus, with my background based on the La Jolla-southern California flora, it was of great interest to find upon first visits to Cabo Colnett, Punta Descanso, and Punta Banda, a number of cold water elements out of keeping with the decreasing latitude. An examination of the then still little-known coastal hydrography of the area revealed that the phenomenon of upwelling was involved, and this led to a ten-year study of the marine vegetation of Pacific Baja California in relation to water temperatures and the occurrence of upwelling (Dawson, 1945b, 1950e, 1951, 1952).

The following general features have now been established by both my own work and that of a number of other investigators, mostly from the Scripps Institution. Under the influence of prevailing winds from the northwest quadrant, upwelling of cold subsurface water occurs discontinuously and with varying intensity and seasonal continuity along the entire Pacific coast of Baja California, except within part of Bahía Vizcaíno and between N. Lat. 24° 50′ and 26°. It reaches its greatest intensity on the south sides of the series of headlands between Punta Baja and Punta Descanso on the far northwest coast. In this region, tongues of cold, upwelled water are prominent below these major headlands and alternate with areas

of relatively warm water between them. The cold waters continue, with only slight latitudinal warming, to well within the reaches of Bahía Vizcaíno, where the configuration of the coast and the submerged shelf impose conditions which result in an eddy system and rapidly increasing surface temperatures. Thus, upwelling ceases near Punta Santa Rosalia, and, along the southern shore of Bahía Vizcaíno, the slow clockwise eddying of the water under high insolation causes high temperatures to obtain, accompanied by characteristic vegetation of tropical character. At Punta Eugenio, however, the abrupt reversal of the trend of the coastline is accompanied by the recurrence of upwelling and an associated cold water flora which prevails southward to Punta Abreojos. Beyond Punta Abreojos, again with the changing trend of the coastline, the intensity of upwelling decreases except for small areas of local prominence south of the Isla Magdalena headlands, and inshore water temperatures slowly rise in keeping with latitudinal warming. Nevertheless, the fact that inshore temperatures are somewhat lower than those well out to sea westward indicates that slight upwelling is still in effect all the way to Cabo San Lucas. Even south of Cabo San Lucas, a tongue of water of somewhat depressed temperature has been detected extending seaward. This seems to demonstrate moderate upwelling and, in part, to explain the relative richness of the algal flora of Cabeza Ballena east of San Lucas within the area of probable maximum intensity.

The islands of Pacific Baja California provide a further range of ecological conditions from those of the mainland. Isla Guadalupe, far west of the influence of coastal upwelling, shows in its high proportion of warm water algal elements the effect of latitudinal warming entirely unlike cold Punta Baja, the nearest mainland point to the east. The *Macrocystis-Egregia* flora does not occur. Islas San Benito, however, where a combination of the cooling influences of upwelling and of warming from insolation obtains, shows a marine flora closely similar to that of La Jolla, 300 miles to the north. Isla Cedros also shows in its various parts marine climatic differences reflecting the mixed influences of cooling and warming factors. Perhaps the most interesting insular conditions are found at the remote pinnacles of Rocas Alijos at N. Lat. 24° 50′, where insolation of the surface waters under the slow southward drift raises temperatures to above 21°C. in November. At these practically inaccessible pinnacles, collections of drift weed and of intact plants from depths of 25 to 90 feet, show the presence at and near the surface of such cool water plants as *Egregia, Macrocystis,* and *Phyllospadix* (representing southern records) and point to a compensatory effect of the exceedingly violent surf in providing necessary amounts of metabolic gases despite the lower solubility in the warmer water (Dawson, 1957). Below the extreme aeration, at depths of 25 to 90 feet, however, a high proportion of tropical species occurs.

As the marine biologist rounds Cabo San Lucas toward the Gulf of California, he encounters rapidly changing ecological conditions within the strict tropics. At Cabeza Ballena, and similarly on all of the islands of the Revillagigedo group to the southwest, reefs occur, bathed by tropical waters of high temperature. These are subject to moderate to heavy surf. The conditions of life are different, under the agitation of breaking waves from the open sea, from those under the calmer conditions one encounters just northward within the edge of the Gulf of California proper at Cabo Pulmo and Punta Frailes. There, relatively protected conditions prevail, and the only coral reef within the area occurs.

The Gulf of California itself is a region of extraordinary ecological diversity, and, moreover, within this diversity there is little duplication of conditions on the Pacific side of the peninsula. The Gulf, in

its upper reaches, is the most isolated large body of water on the Pacific coast. It stretches north through ten degrees of latitude and deeply invades the continent. Its climate is largely a continental climate with extreme temperature variation between winter and summer. It includes a multitude of islands with diverse substrates, exposures, and positions with regard to circulation. Its waters are subject to extreme diversity of tidal amplitude, amounting to a ten-fold increase from south to north. The intertidal region is subject to severe desiccation, high light intensity, and low intensity of surf. These remarkable variations of tide, temperature, circulation, etc., operating on an extreme diversity of shores, from mud flats to rocky cliffs, provide for a flora and fauna as distinctive as for any region of similar size in the world. Some aspects of the relationship between this remarkable environment and the algal flora which has developed will be taken up below.

Throughout the areas of upwelling along Pacific Baja California, and in proportion to the influence of upwelling as opposed to the warming influences of insolation, one finds the characteristic algal species of southern California extending southward. In areas of intense upwelling and strongly depressed temperatures, the intertidal flora more closely resembles that occurring north of N. Lat. 34° in California and includes species not otherwise known to occur intertidally south of central California. To the south of Bahía Rosario, warming influences tempering the upwelling cold gradually eliminate some cold water elements and permit the occurrence of a flora much like that of southern California. At Islas San Benito, 82% of the species are common to La Jolla, California. The California extension, associated with beds of *Macrocystis*, continues south in the upwelling areas to as far as Punta Abreojos. Farther south, *Macrocystis* apparently occurs only sporadically. A moderate complement of California species continues to Punta Pequeña and appears again along the Isla Magdalena headlands, but does not occur prominently southward.

Bahía Vizcaíno is of particular interest, for its south shore in the vicinity of Punta Malarrimo is subject to high temperatures resulting from the absence of upwelling and the presence of high insolation on the eddy system. A number of tropical elements occur here far north of their ranges elsewhere along Pacific Mexico. Another warm water group is common to Guadalupe Island and the southern Bahía Vizcaíno.

Isolated Isla Guadalupe, unaffected by coastal upwelling, has an extremely interesting flora composed of some California species, some tropical Mexican coastal species, some Indo-Pacific insular species, and a conspicuous group of endemics, many of them evidently derived from the California flora, and demonstrating the effectiveness of isolation and divergent ecology on speciation. Rocas Alijos, on the other hand, to judge from the collections available, does not show such endemism on its extremely limited substrate. It would seem regularly to be able to derive contributions to its flora from the mainland to the north, unlike Isla Guadalupe which is too far west for the receipt of regular coastal drift.

Beyond Rocas Alijos we have, in the adjacent sea southwest of Baja California, only the scattered Islas Revillagigedo, of which only Isla Clarion and Isla Socorro have a broadly developed flora (Dawson, 1954c; Setchell and Gardner, 1930; Taylor, 1945). Both of these show the dominance of certain pantropical and Indo-Pacific insular algae, and especially an affinity with the latter in the occurrence of such characteristic forms as the calcareous reef alga *Hydrolithon reinboldii* which is not known to occur along mainland Mexico.

Generally pan-tropical and pan-tropical Pacific species are prevalent along southernmost Baja California and northward to beyond La Paz in the Gulf of California. However, the marine flora is

not richly developed either in diversity of species or in quantity throughout the area south of Isla San Francisco. The best growths are in sandy bays where extensive *Caulerpa* mats occur, while most rocky shores in the vicinity of La Paz, for example, have extremely limited, depauperate floras, at least in the spring season during which they have been observed. A limited, but often conspicuous, element of pan-tropical species continues northward into the Gulf of California, reaching best development in the late spring and early summer. Indeed, some widespread tropical plants such as *Asparagopsis taxiformis, Hydroclathrus clathratus, Chnoospora implexa, Halimeda discoidea, Digenia simplex, Hypnea* spp. occur on the west side of the Gulf, between Santa Rosalia and Isla San Francisco, in dense, luxuriant stands. From Lat. 25 northward, the flora of the Gulf of California is prevailingly a flora of warm water elements associated with *Sargassum* and *Padina*. Among these warm-water plants, pan-tropical and other tropical Indo-Pacific species are frequent. Calcareous green algae are, however, poorly represented. Marine phanerogams are poorly represented by *Ruppia* and *Zostera*. No Laminariales occur in the area, although *Dermarestia* has been taken in the sublittoral. The vegetation is also one of conspicuous endemism, apparently developed through speciation in relative isolation and under the influence of an environment unique for the northeast Pacific. Critical studies have shown, however, that the endemism is not as high as was once supposed.

When Setchell and Gardner (1924) began their initial major treatment of the flora of the Gulf of California, they had only the Johnston collections with which to work and a sketchy knowledge of the region derived mainly from maps. Setchell, as the geobotanist of the team, recognized the isolation of the region and also noted the completely unfamiliar nature of the collection to his experience with the algae of southern California. So distinctive did he consider the flora to be that he assumed the flora of the upper two-thirds of the Gulf of California to be very largely endemic. Upon this premise he and Gardner set about to describe as new species 111 of the 144 entities (77%) recognized in the collection by Johnston. Subsequent field and laboratory studies have proved the falsity of this figure. Critical studies of the writer's collections of 1940 showed that several of the more prominent species in the upper Gulf are identical with well-known Japanese plants. Furthermore, a number of the "new" species described by Setchell and Gardner proved to be only variations of the same species under diverse seasonal and geographic ecological conditions. In other instances, poorly-known, widespread tropical species proved to be among the Gulf of California collections. Altogether it was necessary in the report of the writer's work in 1944 to reduce 30 of the Setchell and Gardner names to synonymy. Reduction of additional names has continued to the present as the identities of Gulf of California plants have progressively been made with those of other parts of the world, particularly of the northwest Pacific. The apparent endemism now stands at about 35%. A comparison of Gulf of California plants with Japanese has shown many of them to be conspecific and this has led to a recognition of a number of Japanese species both in the California and Pacific Baja California floras. Others await more critical study. Thus, Japanese species such as *Pachydictyon coriaceum* occur from central California south along Baja California and also in the Gulf of California; *Lomentaria catenata* occurs both at Isla Magdalena and in the Gulf, while a small group of species such as *Ceramium paniculatum* occurs widely in the Gulf only. Some of these plants clearly suggest very long residence in the eastern Pacific and derivation from Japan by natural means through the clockwise north Pacific circulation. *Lomentaria hakodatensis*, however, occurs in the Gulf, and among

the tropical north Pacific islands as well as in Japan. This may be an example of migration from east to west.

One of the really remarkable species of the northern Gulf of California is *Ishige foliacea,* a well-developed genus of Japan not represented elsewhere in the world. Its abundance in the northern Gulf is best explained to be the result of artificial introduction, naturalization, and rapid spread through effective competition with the native flora. It is assumed that the introduction was effected by transport of viable fragments in ballast water of Japanese fishing boats which operated extensively in the Gulf of California in the early part of the century. The presence of other species of similar Gulf-Japan distribution is probably to be accounted for in this way, but, in the absence of any thoroughgoing surveys of the algae prior to 1921, it is not possible at present to verify such an hypothesis.

Although collections have now been made in a majority of the diverse habitats in the Baja California area, and a large proportion of the entities recognized, we are still far from a complete knowledge of the marine flora, not only as to species distributions, but especially as to affinities and origins. The incompleteness of our knowledge may be pointed out in several ways.

As monographic work continues and it is possible to make critical comparisons of Baja California plants with species from other floras, we continue to find broader distributions for species which were at first supposed to be rather narrow endemics. A good example is *Gracilaria textorii,* a Japanese species recently found by Ohmi (1958) to be identical with *G. vivesii* in the Gulf, this as the result of critical comparison of male plants which had not previously been recognized in Japan. Similarly, it may be found, when adequate comparisons can be made, that among the numerous species of *Sargassum* in the Baja California area, all of them described from the northeastern Pacific, several may be identical with plants of the western Pacific or other tropical or subtropical areas.

Study of a small collection from Isla San Benedicto (Dawson, 1954c), in connection with the volcanic eruption there, revealed some interesting distributional features. A number of widespread tropical, Indo-Pacific distributions appeared, and some with wide distributions but narrow habitats, so that under similar conditions, such as surge-swept offshore rocks awash, the same species appear on opposite sides of the Pacific. More interestingly, one finds at San Benedicto such a species as *Pseudobryopsis hainanensis,* known otherwise only from two collections from the China coast and the Ryukyu Islands. Its occurrence at such widely separated localities can only suggest that a broader and more continuous distribution is present, but has not been recognized because of the extreme sparsity of collections of algae throughout much of the tropical and subtropical Pacific. Thus, vast stretches of coastline along Mexico, central America, and South America have yet to be roughly explored, while only a handful of islands in the central Pacific area have ever been visited by algologists. Even a flora of so accessible an area as our own Hawaiian Islands has yet to be prepared.

Local diversities of ecology are so great that one may easily be misled on the character of the flora of an area by having made too few observations. Thus, an algologist working in the vicinity of Cabo San Lucas is struck by the scarcity of algae on the granitic rocky shores. Only a handful of species are found, and the whole area suggests an impoverished flora. Yet, only a few miles away at Cabeza Ballena, on a volcanic substrate, and under the influence of apparently more favorable circulation, a richly diversified flora occurs in which nearly a hundred entities may be found. Similarly, other extensive areas are known only from single collections, perhaps made at unfavorable seasons or with inadequate equipment. Intertidal collections, for

instance, in the Baja California area may completely falsify the true nature of the flora at depths of a few feet. Thus, for thirty-five years it was thought that *Halimeda* was a rare or incidental element of the Gulf of California, to judge from dredge hauls and intertidal collections. However, work with shallow water diving equipment recently showed that extensive beds of this plant occur in depths which are not accessible either to the intertidal collector or to the ship's dredge.

The advent of self-contained shallow-water diving equipment has, indeed, opened up a whole new field of marine algal exploration. In such areas as the Gulf of California where large tidal amplitude and extreme insolation combine, the intertidal flora generally becomes a specialized one which does not at all truly represent the flora of the richly productive area between 0 and 20 feet. In this inshore area, it has not in the past been possible to work very conveniently or successfully for algae, for ship and launch dredge devices do not serve well on rocky bottoms. Accordingly, in order to obtain a true picture of the nature of the flora, one must see it in position. Such observations have not yet been made on any part of the flora of the upper Gulf of California, but, a year ago, two weeks were spent in observing and collecting with face mask and snorkle in the area of the southwestern Gulf. On that brief cruise (Dawson, 1959), a large number of new records were made for Baja California algae, and, for the first time, something of the composition and richness of the flora of shallow depths was determined. The number of novelties and new records resulting from even such a short period of observation point to our still very limited knowledge in this field.

Similarly, it was only two years ago that Dr. Neushul made the first observations and collections by self-contained diving apparatus along the Pacific coast of Baja California. These collections, made in depths of 20 to 115 feet, are just now being studied. Together with his field notes they constitute a large single advance in our knowledge of the Pacific Coast sublittoral flora, particularly that associated with *Macrocystis* beds.

Finally, something should be said about seasonal variations in the flora of the region. Along Pacific Baja California, the algal flora shows relatively inconspicuous seasonal fluctuation. Many prominent species are present continuously throughout the year although many minor variations in floral composition occur with seasonal growth and decline of individual species. In the northern Gulf of California, there is a prominent alternation of a winter flora with a distinctly different summer flora. Even the dominant sargassums show an alternation of summer and winter species. In the southern Gulf of California and southward along mainland Mexico, the winter flora is extremely poor and the major algal development seems to occur only in summer. Summer collections, however, are all but absent from this region of summer storms. Indeed, throughout all the Baja California area, the majority of collections have been made during the winter-spring season of good sailing weather, and information on summer conditions is notably scant. Accordingly, we are still far from having a complete picture of the marine flora of this region, either geographically or seasonally.

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The Distribution and Affinities of the Littoral Marine Bryozoa (Ectoprocta)

JOHN D. SOULE

Historical Résumé

THE MARINE BRYOZOA (Ectoprocta) of the waters adjacent to Baja California are as yet poorly known. However, within the past few years, the support of the Allan Hancock Foundation, the American Museum of Natural History, and a Grant-in-Aid from the Society of the Sigma Xi, has made possible advances in the systematics and the distribution

of the group within this geographical area.

The earliest work on the ectoproct bryozoans of the Gulf of California region was that of George Busk, appearing as the initial section of the *Catalogue of Mazatlan Mollusca* (P. P. Carpenter), in 1855. The following year, 1856, the same paper, with minor changes in format and content, was published under the heading *Zoophytology*. Of a total of 13 species described in this work, 10 were new. It is regrettable that not all of the species were illustrated.

No further progress was made for 85 years, until 1941, when Steinbeck and Ricketts' *Sea of Cortez* became available. The annotated phyletic catalogue, a part of the appendix, contains a list of seven bryozoans that are identified to species (there are seven others with only generic designations), the work of Ray S. Bassler. As none of the seven species had appeared in Busk's paper, the faunal list of the Bryozoa of the Gulf of California increased to 20.

In 1950, part one of Raymond C. Osburn's *Bryozoa of the Pacific coast of America* was published, adding another 35 species, some of them new, to the faunal list to give a total of 55. Two years later, 1952, part two of Osburn's work added another 63 species, and in 1953, the work of Osburn and of Soule in part three, added another 15 species to the growing list, bringing the total to 133.

Currently, a study, as yet incomplete, resulting from the Puritan-American Museum of Natural History Expedition to the Gulf of California, has disclosed 137 species of Bryozoa in its collection. Forty-four of these are new to the faunal list. At the present time there are at least 177 species of ectoproct bryozoans known from the Gulf of California.

Turning now to the Pacific coast of Baja California, we find the history of the Bryozoa from this region is of very recent origin, reaching back only as far as 1950. Our entire knowledge of the group in this area is between the covers of the work of Raymond C. Osburn referred to above. A census of the bryozoan fauna of this region gives us a total of 120 species.

Current Studies

The Puritan-American Museum of Natural History Expedition commenced its Gulf of California collecting at Mazatlán, Sinaloa, Mexico, then crossed to Bahía Los Frailes, near the tip of Baja California. It then gradually pushed northward, along the Baja side of the Gulf, collecting from island to island, and at several points along the Gulf coast of Baja California. The termination point was San Felipe, Baja California. The nature of the dredging and diving equipment was such that all of the collecting was made well within the limits of the littoral zone. The major part of the littoral collection was in itself within the eulittoral subdivision of 34 fathoms or less, and none of the hauls exceeded 50 fathoms. The Puritan collection and the Hancock collection very nicely supplement one another. The Hancock collection is especially well endowed with material from the northern part of the Gulf, in the vicinity of Isla Tiburon and Isla Angel de la Guarda. The Puritan collection fills in many gaps, and established many new stations in the southern portion of the Gulf.

The study now underway, as was noted in the historical résumé, adds substantially to the number of bryozoan species on the Gulf of California faunal list, as well as augmenting our knowledge of the distribution of the group within the Gulf.

For our knowledge of the Bryozoa from the waters of the Pacific coast of Baja California, we must rely entirely upon the Hancock collection. Numerically, the best represented area is in the region of Isla de Cedros. Of the remainder of the coast, the coverage ranges from adequate to sparse.

Distributional Patterns

The study of the bryozoan fauna of the Gulf of California and that of the Pacific

coast of Baja California reveals some parallels and certain differences.

The southern third of the Gulf of California supports a tropical type fauna. Here 50% of the bryozoans have a well established tropical distribution, 40% are also found in warm temperate waters, and 10% of the known fauna has representatives in cool temperate waters. This tropical area covers a linear distance of about 230 miles, from the region of Cabo San Lucas northward to just north of Isla del Carmen, about 26° North Latitude. Immediately north of the tropical fauna is a region of transition, where the ratio of distribution of tropical and warm temperate species is almost even, with the cool temperate percentage unchanged. In this area the figures are: 46% tropical, 44% warm temperate, and 10% cool temperate representatives. This transitional zone extends for about 150 miles from about 26° North Latitude to 28° North Latitude, in the area just north of Guaymas, Sonora, Mexico. The remaining 300 linear miles of the Gulf of California contains a bryozoan fauna that deviates from the transitional zone, just mentioned, in showing an increase in the percentage of cool temperate forms to 17%. In this northern area, the warm temperate forms drop to 40% and the tropical representatives are reduced to 43%.

A similar break-down of the bryozoan fauna of the Pacific coast of Baja California shows at its southern limit a tropical fauna that contains the following representation: 50% tropical, 34% warm temperate, and 16% cool temperate. This area extends from Cabo San Lucas northward to the region of Bahía de la Magdalena, a linear distance of about 170 miles. A transitional zone, beginning at Bahía de la Magdalena, extends northward to Bahía Tortolo, just south of Punta Eugenio, a linear distance of some 270 miles. In this area, the faunal ratio is: 43% tropical, 42% warm temperate, and 15% cool temperate, paralleling, basically, the transitional area of the Gulf of California. From Punta Eugenio northward to the area of the United States-Mexico border, a linear distance of approximately 350 miles, there is a marked change in the bryozoan faunal representatives, with 27% tropical, 42% warm temperate, and 31% cool temperate.

When we compare the bryozoan fauna of the Gulf of California with that of the Pacific coast of Baja California, the most obvious difference is seen in the character of the northernmost faunal areas of each region. In the Gulf of California, this northern area is dominated, if only slightly, by the tropical representatives. This area may be considered subtropical in its faunal composition. On the Pacific coast of Baja California, in the northern area, a significantly high percentage of cool temperate forms is very much in evidence. In this northern region, the faunal picture is like that found off the coast of southern California, and may be considered warm temperate in faunal make-up.

Faunal Affinities

In establishing faunal affinities, the known bryozoan fauna of the Gulf of California was considered as a unit, and the bryozoan fauna of the Pacific coast of Baja California was considered in like manner. Each of these areas was compared to the known bryozoan faunal composition of the Indo-Pacific region, the Gulf of Mexico-Caribbean region, the Panamic region, and the temperate Pacific coast of North America (from San Diego, California to Puget Sound, Washington). The bryozoan fauna of the Gulf of California has representatives as follows: Indo-Pacific 13%, Gulf of Mexico–Caribbean 19%, Panamic 40%, and Pacific coast temperate 28%. The Pacific coast of Baja California shows: Indo-Pacific 9%, Gulf of Mexico–Caribbean 15%, Panamic 29%, and Pacific coast temperate 47%. Thus, in faunal affinities, the Gulf of California is decidedly Panamic in character, while the Pacific coast of Baja California is strongly Pacific coast temperate.

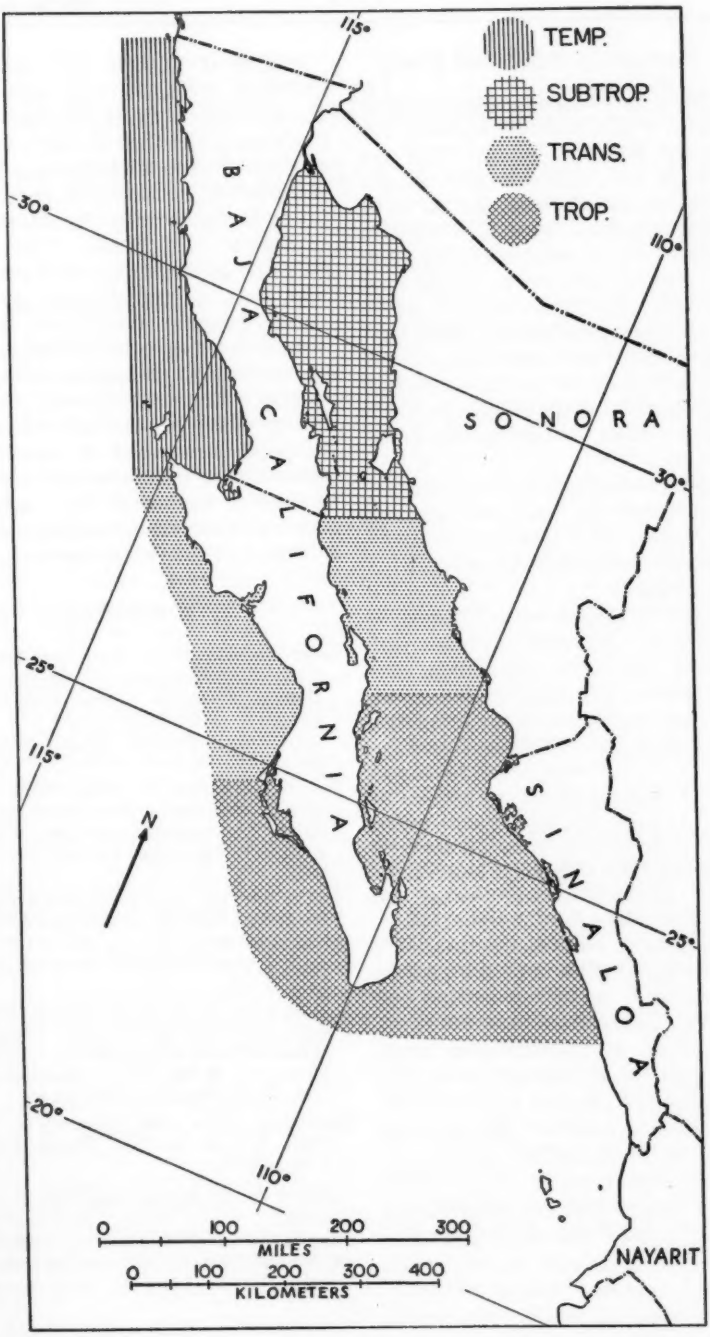

FIG. 1. Zonation of littoral ectoprocts along the coasts of Baja California.

Areas Warranting Additional Study

In the Gulf of California, the one major region that is still practically unknown, in so far as the Bryozoa (Ectoprocta) are concerned, is the littoral region of the Sonora-Sinaloa coast from the area of Puerto Peñasco southward to Mazatlán. In the southernmost reaches of this area, the surface water currents primarily flow in a northerly direction from the open Pacific ocean. It is possible that the faunal picture in the southern coastal region will be more like that of the southern part of the Pacific coast of Baja California, with a gradual transition to the typically Gulf-type fauna.

On the Pacific coast of Baja California, our knowledge of the littoral bryozoans would profit from additional collecting in the area from Punta Eugenio southward to Cabo San Lucas.

In addition to littoral collections, it is felt that deep water dredging in the Gulf of California would be rewarding, especially if the results could be compared to similar deep water hauls made off the Pacific coast of Baja California.

Conclusions

GULF OF CALIFORNIA: The Gulf of California supports a rich bryozoan fauna. The southern portion of the Gulf from the region of Cabo San Lucas northward to the area just above Isla del Carmen (26° N. Lat.) is endowed with a bryozoan population containing a preponderance of tropical forms. This area blends into what is best described as a transitional zone, that extends to the latitude of Guaymas, Sonora, Mexico (28° N. Lat.), and this in turn, gives way to a subtropical type of bryozoan fauna in the northern portion of the Gulf. Considered as a unit, the Gulf of California bryozoan faunal affinities are closest to the bryozoan fauna of the Panamic region.

PACIFIC COAST OF BAJA CALIFORNIA, MEXICO: The bryozoan fauna of the Pacific coast of Baja California, like that of the Gulf of California, may be subdivided into three zones. The southern portion of the coast from Cabo San Lucas to Bahía de la Magdalena supports a tropical type fauna. The area from Bahía de la Magdalena to Punta Eugenio comprises a transitional zone. From Punta Eugenio northward toward the United States-Mexico border, the fauna is the warm temperate type like that off the coast of southern California. The Bryozoa (Ectoprocta) of the Pacific coast of Baja California are allied in their faunal affinities with the bryozoan fauna of the temperate waters of the west coast of North America from San Diego, California, to Puget Sound, Washington.

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Distribution and Affinities of the Brachyuran Crustacea[1]

JOHN S. GARTH

History of Exploration

KNOWLEDGE of the decapod crustaceans, and particularly, of the Brachyura, or short-tailed crabs, of the Baja California-Gulf of California region, goes back barely a century and may be said to date from the early work of John Xantus, who established for the U. S. Coast Survey and maintained, for less than a two-year period, 1859–1861, a tidal gauge station at Cape San Lucas. The specimens that he collected in the immediate vicinity, upon shipment to the U. S. National Museum, became the basis for two fundamental papers by William Stimpson (1860, 1871). A second source were the collections of W. J. Fisher from the Gulf of California and of Henry Edwards from Mazatlán, reported by W. N. Lockington (1877). Regrettably, Stimpson's collections were destroyed in the Chicago fire of 1871, Lockington's in the San Francisco earthquake and fire of 1906. But for the practice of sending syntypes to other institutions, of Stimpson's species to the Museum of Comparative Zoology, Harvard, of Lockington's to the Museum of Natural History, Paris, we would be entirely lacking in specimen material from this early period.

Other collectors who worked either in the littoral or at shallow depths were Verreaux (Saussure, 1853), Diguet (Bouvier, 1895), Orcutt, and Anthony (Rathbun, 1918, 1925, 1930). For the exploration of the deeper waters we are indebted to the U. S. Fish Commission Steamer *Albatross* expeditions of 1887–88 (Rathbun, 1898), of 1891 (Rathbun, 1893), and 1911 (Rathbun, 1923). The modern era of exploration of the Gulf of California may be said to have begun with the California Academy of Sciences expedition in 1921 (Rathbun, 1924) and has been continued by the Templeton Crocker expedition in 1936 (Glassell, 1936; Crane, 1937a, b), and by the Allan Hancock expeditions of 1936, 1937, 1940 (Garth, 1939, 1940), and 1949. Significant contributions have also been made by latter-day independent collectors, among whom should be mentioned H. N. Lowe (Rathbun, 1933), S. A. Glassell (Glassell, 1935), E. F. Ricketts (Steinbeck and Ricketts, 1941), and F. Bonet (Buitendijk, 1950).

The affinities of the brachyuran fauna of the Gulf of California were studied by the late Steve A. Glassell (1934), who noted that "in general it is in the Gulf of California that the tropical species make their most northerly advance on the Pacific coast of North America, although of course some few species have their most northern limits far north of the Gulf." Glassell's study was limited to the brachyuran Crustacea of the three major groups: the cancroid or cyclometopous crabs, the grapsoid or catometopous crabs, and the spider or oxyrhynchous crabs, and was to a large extent a compilation from the literature, in particular, an abstract of information contained in monographs of the late Mary J. Rathbun (grapsoid, 1918; spider, 1925; cancroid, 1930). His personal collecting activities in the Gulf of California and at Magdalena Bay during the 1931–1933 period, however, accounted for 112 species: cancroid crabs 47, grapsoid crabs 32, spider crabs 33, or 56% of the

[1] Allan Hancock Foundation Contribution No. 241.

recorded fauna. Since specific localities were not given for the 46 new records obtained, 18 of which were introductions to the Gulf of California fauna, it has not been possible to credit Glassell with these by citation of published record. However, his careful compilation has proved useful for purposes of comparison and as a point of departure for subsequent faunistic studies.

Including his own collections, the total number of species of the three groups found by Glassell within the Gulf of California (Cape San Lucas to Mazatlán) and at Magdalena Bay on the west coast of Baja California was 197, divided as follows: cancroid crabs 77, grapsoid crabs 54, spider crabs 66. Panamanian species intruding into the Gulf of California region thus bounded numbered 96: cancroid crabs 39, grapsoid crabs 25, spider crabs 32. Species indigenous to the Gulf of California numbered 75: cancroid crabs 27, grapsoid crabs 22, spider crabs 26. Northern species, on the other hand, numbered only 24: cancroid crabs 11, grapsoid crabs 5, spider crabs 8. To recapitulate, of a total of 195 species (eliminating two of doubtful provenience), 96 species, or 48%, were Panamanian, 75 species, or 40%, were indigenous, and 24, or 12%, were of northern origin.

Expeditions subsequent to 1935 that have added materially to our knowledge of the fauna of the region include the *Zaca* expedition of William Beebe in 1936 (Glassell, 1936; Crane, 1937a), the *Velero III* cruises of 1936, 1937, and 1940 (Garth, 1939, 1940), and the *Velero IV* cruise of 1949 (Garth, 1958). As a result of these expeditions, 10 new species, 4 cancroid, 3 grapsoid, and 3 spider crabs, were described, and another 16 species, 5 cancroid, 2 grapsoid, and 9 spider crabs, were recorded for the first time from the Gulf of California. The publication of the fourth monograph on the oxystomatous and allied crabs of America (Rathbun, 1937), and the appearance of the *Zaca* expedition report on the same group of crustaceans (Crane, 1937b), makes it possible to subject this final segment of the marine Brachyura to the same analysis applied by Glassell to the other three.

While the Brachyura of the Allan Hancock Expeditions in the Gulf of California and along the west coast of Baja California have been the subject of continuing studies, these have been reported only in part. Preliminary descriptions of the oxystomatous and allied crabs appeared (Rathbun, 1935) in advance of their monographic treatment (Rathbun, 1937). Similarly, preliminary descriptions of oxyrhynchous or spider crabs appeared (Garth, 1939, 1940) in advance of their comprehensive treatment (Garth, 1958), together with those of the cancroid or cyclometopous crabs, awaiting treatment. The monograph on the cancroid crabs is sufficiently advanced to permit the use of species and locality data with a reasonable degree of confidence. The status of the grapsoid or catometopous crabs, however, is essentially that in which they were left by Rathbun (1918) and by Glassell (1934).

While Glassell recognized both a northern (Californian) and a southern (Panamic) element in the west coast of Baja California-Gulf of California region, he made no attempt to establish faunal boundaries. This was done by the writer in his studies on the warm-temperate fauna on the west coast of North America (Garth, 1955), who pointed out that the intertidal regions of the Gulf of California, from Agua Verde Bay on the west (peninsular) coast to Puerto San Carlos on the east (mainland) coast, constitute in effect a Pacific Mediterranean region, of which the present communication with the ocean, unlike the Strait of Gibraltar, now lies within the tropics. Furthermore, it was pointed out in studies on the brachyuran fauna of Chile and Peru (Garth, 1957) that this warm-temperate fauna had its counterpart in the southern hemisphere, as shown by the existence of species pairs in genera exhibiting tropical discontinuity. Against this background

we may proceed to consider in some detail the distribution of the Brachyura by major groups on the west coast of Baja California, in the Gulf of California, and in islands to the south.

The West Coast of Baja California

The west coast of Baja California, at least in its northern portion, provides a continuum of habitat for north-temperate species found in the littoral zone of southern California south of Pt. Conception. Rocky shore, sandy beach, and muddy lagoon alternate to provide a variety of ecological situations no less hospitable to cold-adapted species than those found north of the United States–Mexico boundary. This favorable environment for temperate species exists at least as far south as Pta. Eugenio, opposite Cedros Island, and locally as far south as Pta. Entrada, outside Magdalena Bay. Since it is within this area that the temperate and tropical faunas meet and mingle, the progress of the northern, and then of the southern element along this coastline will be considered in some detail.

Of the truly boreal crabs, one group of anomurous forms, the family Lithodidae, deserves mention. These were believed to come no farther south than Monterey in the littoral; the deep-water species, such as *Lopholithodes foraminatus* and *Paralithodes rathbuni*, reached the latitude of San Diego (Schmitt, 1921). Within the last decade, however, *Hapalogaster cavicauda* has been collected intertidally at Laguna Beach by Hancock Foundation parties, at Pta. Santo Tomás by William K. Emerson, and at San Geronimo Island by M. Woodbridge Williams; the last two are Baja California localities.

Among the spider crabs, family Majidae, the truly boreal element, comprising the genera *Oregonia, Hyas,* and *Chionoecetes,* has disappeared from the littoral north of Cape Mendocino, California; however, *C. tanneri* has been dredged from near Tanner Bank, on the Mexican border, in several hundred fathoms. A second group of cold-temperate species, including the decorator crabs, *Scyra acutifrons, Loxorhynchus grandis,* and *L. crispatus,* have their southern limit north of Pta. Eugenio and do not occur in the northern part of the Gulf of California. It is the third group, the warm-temperate species, consisting of *Podochela lobifrons* (formerly known as *P. barbarensis*), *Erileptus spinosus,* and *Pyromaia tuberculata,* that are common to southern California-northern Baja California, and Gulf of California waters.

Of the six Pacific American species of kelp crabs of the genus *Pugettia,* four have their southern terminus of range off Baja California: *P. producta* at Santa Rosalia Bay (or Rosarito Point), *P. richi* at San Geronimo Island, *P. dalli* off Thurloe Head, and *P. venetiae* outside Magdalena Bay, while a fifth, *P. hubbsi,* is a Guadalupe Island endemic species. The giant kelp crab, *Taliepus nuttalli,* occurs in *Macrocystis* beds south to Pta. Entrada. None of the larger kelp crabs occur in the Gulf of California, their place being taken by the smaller sargassum crabs, *Acanthonyx petiveri* and *Epialtus minimus.* The controlling factor is here an ecological one, as the kelps themselves are absent from Gulf of California waters.

Of the nine species of crabs of the genus *Cancer,* family Cancridae, found in the American north Pacific, five have their southern limit of range off Baja California: *Cancer gracilis* at Playa Maria Bay, *C. antennarius* at Todos Santos Island, *C. jordani* at Thurloe Head, *C. anthonyi* at Magdalena Bay, and *C. amphioetus* at Magdalena Bay and also in the Gulf of California.

Of the pebble crabs, family Xanthidae, only the genus *Lophopanopeus* ranges north of Monterey, California. The southern limits of range of its three species (as reduced from five by Menzies, 1948) are as follows: *L. bellus diegensis,* San Diego; *L. leucomanus,* Rosarito Beach; *L. frontalis,* Magdalena Bay (as *L. heathi* Rathbun), and also in the Gulf of Cali-

fornia. In addition to *Lophopanopeus*, three other xanthid genera occur in California (excluding *Rhithropanopeus*, a recent introduction to San Francisco Bay). These are *Cycloxanthops*, with *C. novemdentatus* ranging to Pta. Abreojos, *Paraxanthias*, with *P. taylori* ranging to Magdalena Bay, and *Pilumnus*, with *P. spinohirsutus* ranging to Pta. Entrada, outside Magdalena Bay, and a cognate species, *P. townsendi*, inside Magdalena Bay and in the Gulf of California.

Among the grapsoid crabs of the family Grapsidae, the lined shore crab, *Pachygrapsus crassipes*, has its southern limit at Santa Margarita Island and occurs also in the Gulf of California. The closely related species of *Hemigrapsus*, *H. nudus* and *H. oregonensis*, have their southern limits at Turtle Bay and Todos Santos Bay (Rathbun, 1923), respectively. The latter, as reported from the Gulf of California by Rathbun (1918), was later determined by her to be a new species, *Goetice americanus* (Rathbun, 1923).

It will have been noted that when a north-temperate genus is represented in the Gulf of California it is by a single species only, and that where this genus is represented by several species on the west coast of Baja California, it is the species with the most southerly terminus of range that occurs in the Gulf of California. This is true in *Cancer* of *C. amphioetus* and in *Lophopanopeus* of *L. frontalis*. It would be true of *Hemigrapsus* if *Goetice americanus* = *Hemigrapsus oregonensis* as originally identified by Rathbun. It is also noticeable that when the Gulf of California range of these species is compared with their west coast of Baja California range, the southern limit in the Gulf of California is almost always farther north than on the open Pacific coast. This corresponds with what is known of temperatures in the region, as the outer coast is under a northerly current regime, with frequent upwelling, while the Gulf of California is cut off from northerly currents, with upwelling and associated phenomena modified by local conditions.

The similarity of the warm-temperate faunas of northern Baja California and of the Gulf of California suggested to the early naturalists past water connections between them. These have been placed variously: at the level of the Magdalena Plain, at the mid-peninsular level below the Sierra Vizcaíno, or above the Sierra Vizcaíno at the level of Scammon Lagoon. While each of these situations can be shown to have existed in the geological past, it is not necessary to go beyond the Pleistocene to explain the present distribution. A slight southward displacement of present-day isotherms, coupled with such rises in sea level as are known to have occurred interglacially, would again unite the warm-temperate faunas of the two regions.

Let us now consider the tropical fauna of this same coastline, starting at Magdalena Bay and tracing its progress northward (Fig. 1). Magdalena Bay and adjacent Almejas Bay possess a richly developed tropical fauna, consisting for the most part of species ranging continuously to Panama and beyond. The spider crabs, families Majidae and Parthenopidae, are represented inside Magdalena Bay by no less than 24 species, with two additional in Santa Maria Bay, on the outer coast at the same latitude. (It will be remembered that it is at Pta. Entrada, outside Magdalena Bay, that the northern species, *Taliepus nuttalli*, *Epialtus hiltoni*, and *Pachygrapsus crassipes*, make their last stand coming south.) Of these 26 species, only six range north of Pta. Eugenio, and of these *Pitho picteti* and *Inachoides laevis* drop out at Scammon Lagoon, *Pelia tumida* drops out at San Pedro, *Erileptus spinosus* at Santa Barbara, *Podochela hemphilli* at Monterey Bay, and *Pyromaia tuberculata* continues to Monterey Bay and Tomales Bay, north of San Francisco.

The cancroid crabs, families Portunidae, Cancridae, and Xanthidae, are represented at Magdalena Bay by 10 species,

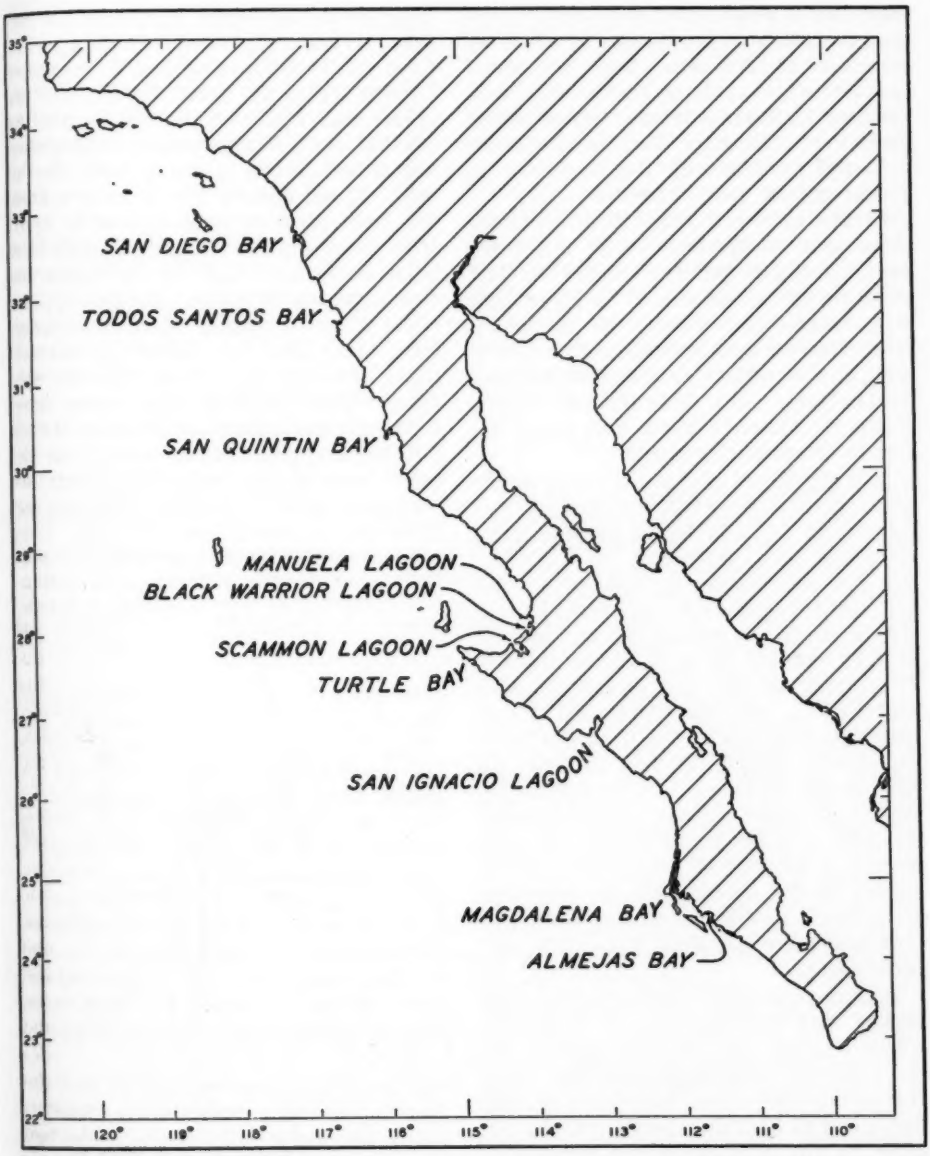

FIG. 1. The peninsula of Baja California, showing the west coast bays and lagoons that serve as refuges for warm-water relict species.

plus an additional six species in Santa María Bay, outside. Of these 16 species, 10 range farther north, and of these *Leptodius occidentalis* drops out at San Ignacio Lagoon, *Eurytium affine* at Turtle Bay, *Callinectes bellicosus* at San Diego

Bay, *Cancer amphioetus* and *Lophopanopeus frontalis* at Newport Bay, *Callinectes arcuatus* at Anaheim Bay, *Pilumnus spinohirsutus* at San Pedro, *Portunus xantusii* at Santa Barbara, *Paraxanthias taylori* at Monterey Bay, and *Cancer anthonyi* at Monterey Bay and Bodega Bay, north of San Francisco.

Of the grapsoid crabs, families Grapsidae and Ocypodidae, the mangrove crab, *Goniopsis pulchra,* makes its last stand on Mangrove Island in Magdalena Bay, where also occurs the mangrove crab, *Sesarma magdalenense.* The fiddler crab, *Uca crenulata,* occurs at Magdalena, Santa María, San Quintín, San Diego, Newport, Alamitos Bays, and Playa del Rey in estuarine situations.

It is significant that the most northerly occurrence of these tropical or semitropical species is in a protected bay or lagoon, sheltered from upwelling by a shallow sill, and with maximum insolation present, while the nearest unprotected situation in which the species is found may be several hundred miles to the southward. It is apparent that the present tropical relicts of the west coast bays and esteros may date from no earlier than the latest interglacial period. If this be true, we have in the difference in temperature between the outer coastal waters opposite the present relict location and the most northerly locality at which the species occurs in the open ocean an empirical measure of the displacement of isotherms that has occurred since the range was continuous.

Recent exploration of the Vizcaíno Bay region, and in particular, of Scammon, Black Warrior, and Manuela lagoons, by the *Velero IV,* the Kenyon-Williams, and the Knudsen-Gorsline (*Horizon*) expeditions, has yielded unexpected results, insofar as the Brachyura are concerned. From Vizcaíno Bay itself have come the spider crab, *Microphrys platysoma,* dredged at Pta. Malarrimo, and the xanthid crab, *Eurypanopeus planissimus,* collected intertidally at North Bay, Cedros Island. From Lagoon Head anchorage (Fig. 2) on seaweeds, has come the sargassum crab, *Epialtus minimus,* while from shallow dredging inside Scammon Lagoon (Fig. 3) itself have come the spider crab, *Podochela latimanus,* and the xanthid crab, *Hexapanopeus rubicundus,* which last occurs in San Quintín Bay as well. These species are unknown from the west coast of Baja California apart from these unpublished records, and have been considered Gulf of California endemic species. Moreover, the three spider crabs show a degree of differentiation from their Gulf of California counterparts, although at no more than the subspecies level. If these were widely ranging southern California-west coast of Baja California species found isolated in the upper part of the Gulf of California, we would recognize a familiar situation and know how to treat it taxonomically. They are, however, widely ranging Gulf of Cali-

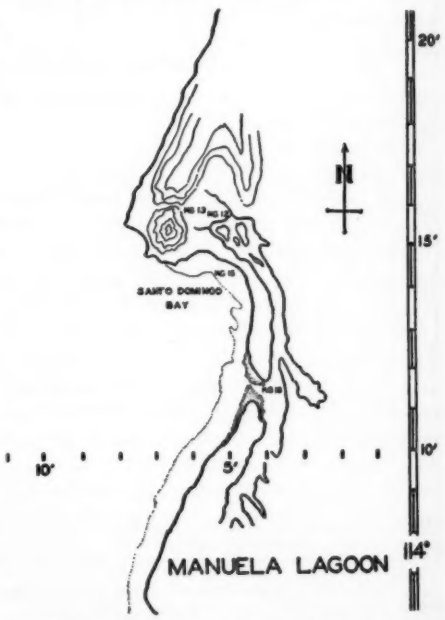

FIG. 2. Manuela Lagoon, in the Vizcaíno Bay region, showing Knudsen-Gorsline stations. The Gulf of California sargassum crab, *Epialtus minimus,* was obtained here, at 28° N. Latitude.

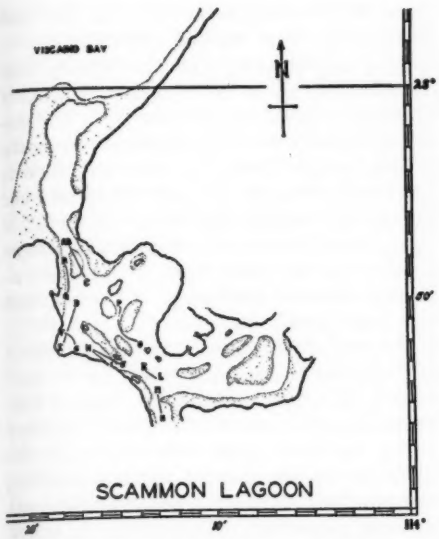

FIG. 3. Scammon Lagoon entrance from Vizcaíno Bay, showing dredge stations at which the Gulf of California species, *Podochela latimanus* and *Hexapanopeus rubicundus*, were collected.

fornia species found isolated in a few west coast lagoons. In this case the pattern of the interglacial relicts of the more northerly bays and estuaries suggests an explanation: are not these also the relicts of an earlier advance up the west coast of warm-water species for which suitable temperature conditions no longer exist on the unsheltered peninsula, but for which the temperature regime of these sheltered bays, as of the Gulf of California, remains ideal? The fact that most of them represent tropical, rather than temperate, genera lends credence to this view.

In concluding the presentation of distribution of Brachyura on the Pacific coast of Baja California, it may be stated by way of summary: (1) that the region between Pt. Conception, California, and Pta. Entrada, Baja California, constitutes a transition area between the north-temperate and tropical marine faunas; (2) that within this area cold-water species are found in progressively diminishing numbers from north to south, clinging most persistently to rocky headlands, where upwelling occurs; (3) that within this area warm-water species are found in progressively smaller numbers from south to north, frequently making their last stand in a shallow bay or estuary where insolation is present, separated by a discontinuity of tens or hundreds of miles from their next most northerly occurrence in the open ocean; and (4) that this discontinuity gives an empirical measurement of the displacement of isotherms that has occurred since the time of continuous range.

The Gulf of California

The Gulf of California presents a special problem, extending as it does well north of the latitude of Cedros Island and enclosing a body of water which at its northern end is temperate (but with high summer temperatures), while its southern end and only present communication with the Pacific lies well within the tropics. It has generally been considered as supporting a Panamic fauna only, although Hubbs (1948; 463) mentions dilution of Panamic types with California coastal types of fishes in its upper portion. Southern California-northern Baja California coastal types of Brachyura found in the Gulf of California include the following: among the oxystomes, *Hepatus lineatus* and *Randallia ornata;* among the spider crabs, *Podochela lobifrons* (formerly known as *P. barbarensis*) and *P. hemphilli, Pyromaia tuberculata,* and *Erileptus spinosus;* among the cancroid crabs, *Cancer amphioetus, Lophopanopeus frontalis,* and *Pilumnoides rotundus;* and among the grapsoid crabs, *Pachygrapsus crassipes* and *Uca crenulata.* Differentiation of the Gulf population from that of the outer coast varies from none at all in the case of *Pachygrapsus crassipes* through populational in the case of *Randallia* (where the Gulf population, described as a full species, *R. angelica,* is not

now thought to be so), to subspecific in the case of *Pyromaia* (where *P. mexicana* was removed from synonymy and established as a subspecies of *P. tuberculata*), to full species in the case of the *Libinia setosa-L. mexicana* species pair. The degree of differentiation seems to be related to the temperature tolerance of the species concerned: the eurythermic and widely ranging species are undifferentiated, the stenothermic and narrowly ranging species are most completely differentiated. This leads us to a consideration of the Gulf of California endemic species.

Among the spider crabs, family Majidae, two well-defined forms are restricted to the upper portion of the Gulf of California. One, *Libinia mexicana,* occurs from Rocky Point (Pta. Peñasco) south to San Felipe on the peninsula side and to San Ignacio Bay, Sinaloa, on the mainland side, and has as its cognate *L. setosa* of the west coast of Baja California. The other, *Pyromaia tuberculata mexicana,* occurs from Rocky Point south to Willards Point on the peninsula side and to outside Guaymas on the mainland side, and is clearly a geographical segregate of the widely ranging *P. t. tuberculata.* Other species taken at Rocky Point, or at least as far north as Puerto Refugio, Angel de la Guarda Island, range southward as follows: *Podochela latimanus* and *Epialtus minimus* to La Paz Bay (and on the west coast at Scammon Lagoon), *Stenocionops beebei* to Puerto Escondido (and at Santa María Bay), *S. angusta* (formerly known as *S. contigua*) to San Lorenzo Channel (and at Magdalena Bay), *Eucinetops lucasi* and *Collodes tumidus* to Cabeza Ballena (the latter at Magdalena Bay and east of Cedros Island). Three other species appear to be restricted to the southern portion of the Gulf: *Herbstia camptacantha* from Patos Anchorage to San Gabriel Bay, Espíritu Santo Island (extralimital at Tangola-Tangola), *Epialtus sulcirostris* from San Marcos Island to Cabeza Ballena, and *Hemus analogus* from Isla Partida to San Gabriel Bay (and Tenacatita Bay on the mainland).

The spider crabs of the family Parthenopidae have not developed Gulf of California endemic species, with the possible exception of *Parthenope triangula,* which ranges from Puerto Escondido to off Los Frailes on the peninsula side and occurs in Magdalena Bay. However, it ranges via Socorro, Clarion, and Galápagos Islands to La Plata Island, Ecuador, although it has not been collected from the mainland.

Of some 21 species of cancroid crabs of the family Xanthidae that have their center of distribution in the Gulf of California, eight, or over a third, are restricted to its northern part. These include five with extremely limited ranges centering around San Felipe: *Panopeus diversus,* known also from Cholla Bay! (! = new record); *Neopanope peterseni,* Angeles Bay! to Puerto San Carlos; *Eurypanopeus confragosus, Eurytium albidigitum,* and *Pilumnus tectus,* collected so far only at San Felipe. The other three range farther south, but in no case farther than North Bay, San Francisco Island: *Glyptoxanthus meandricus,* Punta Peñasco to San Francisco Island! and outside Guaymas!; *Eurypanopeus ovatus,* San Felipe! to Puerto Escondido! and outside Guaymas!. None of these species occur on the west coast of Baja California, insofar as is known.

Another group of eight species ranges throughout the Gulf and frequently beyond its confines. These are *Leptodius occidentalis,* San Luis Gonzales Bay to Punta Trinidad! (and on the west coast north to San Juanico Bay and San Ignacio Lagoon!), *Lophopanopeus frontalis,* Rocky Point! to La Paz (and north to Santa Monica Bay), *Eurypanopeus planissimus,* Tepoca Bay! to Punta Trinidad! (and Magdalena Bay and North Bay, Cedros Island), *Eurytium affine,* San Luis Gonzales Bay to Pichilinque Bay (and at Magdalena Bay and Turtle Bay), *Pilumnus townsendi,* Adair Bay to La Paz

(and Magdalena Bay), *Hexapanopeus rubicundus,* San Felipe to La Paz! (and at Scammon Lagoon and San Quintín Bay!), *Micropanope areolata,* Rocky Point! to Los Frailes! (and San Juanico Bay!). *Leptodius occidentalis* and *Eurytium affine* occur also as vagrants in the Galápagos Islands, but are not found on the mainland south of Manzanillo, being replaced there by Panamic species.

Another group of four species occurs in the southern portion of the Gulf only. These are *Micropanope cristimana* and *Pilumnus stimpsoni,* Cape San Lucas and Manzanillo; *Paraxanthias insculptus,* Cape San Lucas and Galápagos; and *Micropanope nitida,* Salinas Bay, Carmen Island! to La Paz Bay!.

The cancroid crabs of the family Portunidae, or swimming crabs, have two Gulf of California endemic species: *Portunus minimus,* Tiburon Island to Tres Marias Islands, and *P. pichilinquei,* Cape Tepoca to Pichilinque Bay (and Magdalena Bay on the outer coast). However, the exhaustive series in the Hancock collections suggests that these may represent but a single species.

The grapsoid crabs of the family Goneplacidae are mud dwellers and it is not surprising to find them prominent in the upper Gulf fauna. *Oediplax granulata* and *Panoplax mundata* both occur in the vicinity of Consag Rock, while *Trizocarcinus dentatus* is found from Pta. San Fermin to Cape Lobos, and also at Espíritu Santo Island. Of these only *Oediplax granulata* occurs on the west coast of Baja California, at Pta. Tosco. *Chasmocarcinus ferrugineus,* described from Pta. Arena, is believed to be synonymous with the Panamic *C. latipes.* (See Garth, 1940.)

The grapsoid crabs of the family Pinnotheridae are commensals found in association with mollusks, annelids, and echinoderms. The 18 species occurring in the Gulf of California as endemics reflect the indefatigable efforts of the late S. A. Glassell; their "distribution" is the pattern of his collecting localities. Of this number 10 have been collected only at San Felipe and/or Rocky Point and must tentatively be classified as upper Gulf species. Three more, known only from San Felipe or Rocky Point in the Gulf but occurring also at Magdalena Bay, suggest a wider Gulf of California distribution. Two, known only from Pichilinque Bay, are tentatively considered southern; one known only from Mulegé Bay might be either northern or southern. The ranges of their commensal hosts will define their ultimate distribution.

The grapsoid crabs of the family Cymopoliidae yield two endemic species of general distribution: *Cymopolia zacae,* Puerto Refugio to Cape Pulmo, and *C. zonata,* Puerto Refugio to Cabeza Ballena on the peninsular side, Tiburon Island to Ensenada de San Francisco, outside Guaymas, on the mainland side (and at Magdalena Bay on the west coast). A third species, *C. cortezi,* described from Puerto Escondido, has been collected at Wenman Island in the Galápagos. Like the Goneplacidae, the Cymopoliidae are dredged.

The grapsoid crabs of the family Grapsidae have two Gulf endemics, *Cyclograpsus escondidensis,* Gonzaga Bay to Puerto Escondido, and *Goetice americanus,* [San Luis] Gonzales Bay to Georges Island (and at San Bartolomé Bay on the outer coast). *Sesarma magdalenense* is a Magdalena Bay endemic, occurring there on mangrove trees.

The grapsoid crabs of the family Ocypodidae have two Gulf endemics, *Uca coloradensis* and *U. monilifera,* both confined to the mouth of the Colorado River.

Although perhaps of greater interest from an evolutionary and distributional standpoint, it is neither the Gulf of California endemics nor the southern California-northern Baja California coastal types that predominate throughout most of the Gulf, but the vastly greater array of species that have invaded the region from the American tropics, many of

which range continuously to Panama and beyond. In an attempt to define the distribution of Panamic species in the Gulf of California, the advance of each up both the mainland and peninsular east coast was traced; the endpoints were established from Hancock expeditions records, supplemented by published records of other expeditions. Since the data are voluminous, they are presented in a series of tables that include, for purposes of comparison, the advance of these species up the peninsular west coast as well. A résumé by families is here given:

Of the spider crabs of the family Majidae (Table I) 37 Panamic species are present, 32 of them on the mainland side and 31 of them on the peninsular side of the Gulf of California, with 12 on the peninsular west coast. Of these 37 species, 19, or more than half, are present north of a line drawn from San Francisco Point to the south end of Tiburon Island, where the Gulf conspicuously narrows. Of the 12 species that reach Puerto Refugio, Angel de la Guarda Island, 11 are normally dredged, while the single shore species, *Ala cornuta*, continues with three dredged species to Rocky Point. This suggests that the Panamic shore species are first to drop out; however, it should be borne in mind that the greater tidal amplitudes of the upper Gulf tend to obscure the usually sharp demarcation between intertidal and subtidal zones.

Of the spider crabs of the family Parthenopidae (Table I) 11 Panamic species are present, eight on the mainland side and nine on the peninsular side of the Gulf of California, with six on the peninsular west coast. Of these 11 species, six, or over half, attain a line drawn from San Marcos Island diagonally northward to Guaymas, somewhat south of the narrows. The family is a tropical one, with but one north-temperate species, *Heterocrypta occidentalis*, on the west coast.

Of the cancroid crabs of the family Portunidae (Table II) 11 Panamic species are present, 10 on the mainland side, six on the peninsular east side, and five on the peninsular west side. Of these 11 species, four come no farther north than Isabel Island or Punta Piaxtla (Mazatlán), but only one of them crosses the Gulf to Los Frailes. Only four of the 11 are present at Guaymas, and of these *Arenaeus mexicanus* continues to Tepoca Bay on the east side and *Callinectes bellicosus* to San Felipe on the west side of the Gulf, reflecting the difference in their ecological preferences, the former for open sandy beaches, the latter for protected lagoons.

Of the cancroid crabs of the family Xanthidae (Table II) 33 Panamic species are present, 27 on the mainland side and 29 on the peninsular side of the Gulf of California, with 12 on the peninsular west coast. Of the 27 from the mainland side, 13, or nearly half, are unrecorded from north of Isabel Island or Tres Marías Islands; however, peninsular records are available for 12 of the 13, possibly because the mainland coast between Banderas Bay and Guaymas has been insufficiently collected. While this is true enough, another explanation seems plausible. When the ecology of these 13 xanthid species is considered, it is found that eight of them inhabit the *Pocillopora* coral colony exclusively, while at least three more are frequently encountered in this habitat. Could it not be that the heavy surf that precludes landing along this unprotected, sandy coast has produced conditions that are unfavorable for the establishment of stony corals also?

Of the 29 species represented on the peninsular side, 16, or more than half, are still present at Puerto Escondido. Seven species occur from San Marcos Island north, of which one, *Eriphia squamata*, persists in the intertidal zone to San Felipe and to Rocky Point. The family is highly developed in the tropics and includes a large proportion of the coral commensals. With the exception of *Carpilodes cinctimanus*, taken recently at Puerto Escondido, these come no farther north than Espíritu Santo Island.

Of the grapsoid crabs of the family

TABLE I—PANAMIC SPECIES OF MAJOIDEA OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
MAJIDAE				
Eucinetops panamensis		Angel de la Guarda I.	Tiburon Island	S
Euprognatha bifida	San Benito Islands	Angel de la Guarda I.	Tepoca Bay	D
Collodes granosus		Los Frailes	Pta. Piaxtla	D
Collodes tenuirostris	Cedros Island	Puerto Refugio	Tepoca Bay	D
Paradasygyius depressus		Concepción Bay	Ensenada de San Francisco	D
Pyromaia t. tuberculata	(Tomales Bay)	Puerto Refugio	Tiburon Island	S–D
Inachoides laevis	Cedros Island	Puerto Refugio	Rocky Point	D
Podochela vestita	Santa María Bay	Angel de la Guarda I.	Rocky Point	D
Podochela veleronis		Los Frailes	Isabel Island	D
Stenorynchus debilis		Consag Rock	Tepoca Bay	S–D
Pitho sexdentata		Pta. Marcial Reef	Tiburon Island	S–D
Pitho picteti	Scammon Lagoon	Concepción Bay	Tepoca Bay	S–D
Tyche lamellifrons		Agua Verde Bay	Isabel Island	S–D
Sphenocarcinus agassizi		Puerto Refugio	San Pedro Nolasco	D
Acanthonyx petiverii	Santa María Bay	La Paz Bay	Mazatlán	S–D
Eupleurodon trifurcatus		Cabeza Ballena	(Acapulco)	S
Notolopas lamellatus			Rocky Point	S–D
Notolopas mexicanus			Pta. Piaxtla	S–D
Neodoclea boneti			Macapule	D
Lissa tuberosa	Magdalena Bay	Tortuga Island	Tres Marías	D
Lissa aurivilliusi	Santa María Bay	Puerto Refugio	(Tenacatita)	D
Ala cornuta		Puerto Refugio	Cholla Bay	S–D
Mithrax tuberculatus		Carmen Island	Tres Marías	S–D
Mithrax armatus		Los Frailes	Mazatlán	S
Mithrax sinensis		Puerto Refugio	San Esteban	S–D
Mithrax pygmaeus			Isabel Island	S–D
Mithrax spinipes		Agua Verde Bay		S–D
Mithrax denticulatus		Agua Verde Bay	Isabel Island	S
Teleophrys cristulipes	Santa María Bay	Agua Verde Bay	Isabel Island	S–D
Microphrys platysoma	Malarrimo Point	Puerto Refugio	Tiburon Island	S–D
Microphrys triangulatus		Concepción Bay	Isabel Island	S–D
Microphrys branchialis	Dewey Channel	Angeles Bay	Isabel Island	D
Stenocionops ovata			Tiburon Island	D
Macrocoeloma villosum		Agua Verde Bay		S–D
Macrocoeloma maccullochae			Isabel Island	D
Hemus finneganae		Puerto Refugio		S–D
Thoe s. sulcata		Puerto Refugio	Tiburon Island	S–D
PARTHENOPIDAE				
Parthenope exilipes		Boca de la Trinidad		D
Parthenope depressiuscula			Isabel Island	D
Parthenope triangula	Magdalena Bay	Puerto Escondido		D
Parthenope excavata		Puerto Refugio	Isabel Island	D
Parthenope stimpsoni			Isabel Island	D
Thyrolambrus glasselli	Magdalena Bay	San Marcos Island	(Tenacatita)	D
Solenolambrus arcuatus		Los Frailes	Tepoca Bay	D
Leiolambrus punctatissimus	Point Tosco	Cabeza Ballena	Off San Blas	D
Mesorhoea belli	San Juanico Bay	Puerto Refugio	Georges Island	D
Cryptopodia hassleri	Santa María Bay	Puerto Refugio	Ensenada de San Francisco	D
Heterocrypta macrobrachia	Santa María Bay	Consag Rock	Rocky Point	D

S = shore-collected D = dredged

TABLE II—PANAMIC SPECIES OF CANCROIDEA OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
PORTUNIDAE				
Portunus acuminatus			Isabel Island	D
Portunus asper			Pta. Piaxtla	D
Portunus affinis			Isabel Island	D
Portunus tuberculatus		Los Frailes	Isabel Island	D
Portunus iridescens	Santa María Bay	Santa Inez Bay	San Ignacio Bay	D
Callinectes bellicosus	Scammon Lagoon	San Felipe	Puerto San Carlos	S–D
Callinectes arcuatus	Manuela Lagoon	Espíritu Santo I.	Guaymas	S–D
Callinectes toxotes		Cape San Lucas		S–D
Arenaeus mexicanus	Santa María Bay	Puerto Escondido	Tepoca Bay	D
Cronius ruber	Cedros Island		Guaymas	S–D
Euphylax robustus			Yavaros	
ATELECYCLIDAE				
Pliosoma parvifrons	Santa María Bay	Los Frailes		D
Kraussia americana		Puerto Refugio		D
CANCRIDAE				
Cancer porteri			Rio San Lorenzo	D
XANTHIDAE				
**Carpilodes cinctimanus*		Puerto Escondido	Isabel Island	S
Platypodia rotundata	Santa María Bay	Salinas Bay	Bahía Catalina	S
Actaea dovii		San Francisco I.		S
Actaea sulcata		Espíritu Santo I.	Tiburon Island	S–D
Lipaesthesius leeanus		San José Island	Tiburon Island	D
Medaeus lobipes	Santa María Bay	Cape Pulmo	San Ignacio Bay	D
**Medaeus spinulifer*		Fraile Bay		S–D
Medaeus pelagicus	Magdalena Bay	Consag Rock	San Pedro Nolasco	D
**Daira americana*		Carmen Island	Isabel Island	S–D
Cycloxanthops vittatus		Carmen Island	Puerto San Carlos	S–D
Xanthodius sternberghii	Magdalena Bay	Willard Point	George Island	S
Xanthodius stimpsoni		Espíritu Santo I.	Tres Marías Ids.	S–D
Lophoxanthus lamellipes		Puerto Escondido	Tres Marías Ids.	S–D
Hexapanopeus orcutti			Topolobampo	S–D
Hexapanopeus sinaloensis	Santa María Bay			D
Lophopanopeus maculatus		San Marcos Island		D
Panopeus chilensis			Guaymas	S
Panopeus purpureus	Cedros Island	San Felipe		S
Panopeus bermudensis	San Ignacio Lagoon	Puerto Escondido	Guaymas	D–S
**Micropanope xantusii*		Partida Island	Isabel Island	S–D
Micropanope polita	Guadalupe Island	Puerto Refugio	Tiburon Island	D
Micropanope lata	San Jaime Bank		San Pedro Nolasco	D
Micropanope armstrongi	Santa María Bay			D
Pilumnus limosus		Gonzaga Bay	Tiburon Island	S
Pilumnus pygmaeus	Santa María Bay	San Marcos Island	Isabel Island	S–D
Pilumnus stimpsoni		Los Frailes		D
**Heteractaea lunata*		Agua Verde Bay	Isabel Island	S–D
Heteractaea peterseni		San Francisco I.		D
Ozius verreauxii			Isabel Island	S
Ozius perlatus		Cabeza Ballena	Isabel Island	S
Epixanthus tenuidactylus		Concepción Bay	Isabel Island	S–D
Eriphia squamata	San Juanico Bay	San Felipe	Cholla Bay	S
**Domecia hispida*		Espíritu Santo I.	Isabel Island	S–D
**Trapezia cymodoce ferruginea*		Espíritu Santo I.	Isabel Island	S–D
**Trapezia digitalis*		Espíritu Santo I.	Isabel Island	S–D

* Inhabitant of the *Pocillopora* coral colony.

Goneplacidae (Table III) eight Panamic species are present, four on the mainland side, five on the peninsular east coast, and five on the peninsular west coast. Of the eight species, two barely enter the Gulf of California, one reaches Angel de la Guarda Island, while four persist to San Felipe, Consag Rock, or Rocky Point.

Of the grapsoid crabs of the family Pinnotheridae (Table III) six Panamic species are present, two on the mainland side, three on the peninsular east coast, and one on the peninsular west coast. Of these *Pinnixa transversalis,* commensal in worm tubes, is most persistent, continuing to San Felipe and Rocky Point.

Of the grapsoid crabs of the family Cymopoliidae (Table III) two Panamic species occur in the Gulf. Of these *Cymopolia fragilis* is more widely distributed, occurring on all three coasts, while *C. lucasii* appears limited to the peninsular east coast.

Of the grapsoid crabs of the family Grapsidae (Table III) nine Panamic species are present, five on the mainland coast, eight on the peninsular east coast, and five on the peninsular west coast. Of the eight species, three barely enter the Gulf at Isabel Island or Cape San Lucas, one reaches Concepción Bay, while two persist to Guaymas and beyond. Best known and most conspicuous, *Grapsus grapsus* was found by Hancock Expeditions north to San Esteban Island, in the aforementioned narrows. [As "Sally Lightfoot" it is mentioned as occurring at Puerto Refugio by Steinbeck and Ricketts (1941; 225), albeit in the narrative rather than in the systematic section.] Although found north to Cedros Island on the peninsular west coast, *Pachygrapsus transversus* comes no farther north than Espíritu Santo Island on the peninsular east coast. The mangrove crab, *Goniopsis pulchra,* drops out at Espíritu Santo Island and at Magdalena Bay, on the east and west peninsular coasts, respectively, but occurs at Guaymas on the mainland.

Of the grapsoid crabs of the family Gecarcinidae (Table III), the land crabs, *Gecarcinus planatus* comes north to San Ignacio Bay, Sinaloa, *Ucides occidentalis* to Espíritu Santo Island, and *Cardisoma crassum* to Agua Verde Bay. None of these occurs on the west side of Baja California, insofar as is known.

Of the grapsoid crabs of the family Ocypodidae (Table III), the ghost crab, *Ocypode occidentalis,* is found on sandy beaches at Agiabampo on the mainland, at Carmen Island on the peninsular east coast, and north to Todos Santos Bay on the peninsular west coast. Of seven Panamic species of fiddler crabs, genus *Uca,* three occur on the mainland north to Guaymas and vicinity, four on the peninsular east coast, of which one reaches Carmen Island, and three on the peninsular west coast, of which one reaches San Bartolomé Bay.

In conclusion, it may be stated that the northern limit of the Panamic fauna in the Gulf of California cannot presently be defined because the dropping out of tropical species is gradual and occurs throughout its entire length, with 50% of the Panamic species still present in its upper portion. It is also apparent that the region immediately north of the narrows has the greatest rate of species change.

Insular Species

In an earlier paper (Garth, 1946) attention was called to the 11 species of Brachyura common to the Gulf of California and the Galápagos Islands, but not found along the mainland from the Gulf of California to Ecuador. Such species, comprising 9% of the Galápagos brachyuran fauna, were believed to have been transported in the larval stage by the southerly directed California current and the eastwardly directed Equatorial counter current. Significantly, they represent a larger fraction of the Galápagos brachyuran fauna than the five species, or 4%, common to the Galápagos Islands

TABLE III—PANAMIC SPECIES OF GRAPSOIDEA OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
GONEPLACIDAE				
Chasmocarcinus latipes	Cedros Island	Angel de la Guarda		D
Chasmophora macrophthalma	Point Tosco	Gorda Point		D
Cyrtoplax panamensis		San Felipe	Isabel Island	D
Euryplax polita			Isabel Island	S–D
Glyptoplax pugnax				
Prionoplax ciliata	Point Tosco			D
Speocarcinus californiensis	(Mugu Lagoon)	Gonzaga Bay	Rocky Point	S–D
Speocarcinus granulimanus	Cedros Island	Consag Rock	Rocky Point	D
PINNOTHERIDAE				
Dissodactylus nitidus	Abreojos Point	Concepción Bay		S
Pinnixa affinis				
Pinnixa transversalis		San Felipe	Rocky Point	D
Pinnotheres lithodomi				
Pinnotheres margarita		Mulegé Bay		S
Pinnotheres orcutti			Tres Marías Ids.	
CYMOPOLIIDAE				
Cymopolia fragilis	Cedros Island	Inner Gorda Bank	Guaymas	D
Cymopolia lucasii		Angel de la Guarda		D
GRAPSIDAE				
Aratus pisonii	Magdalena Bay		Isabel Island	S
Geograpsus lividus		San Francisquito	Santa Barbara	S
Goniopsis pulchra	Magdalena Bay	Espíritu Santo I.	Guaymas	S
Grapsus grapsus	San Benito Ids.	Puerto Refugio	Tiburon Island	S
Pachygrapsus transversus	Cedros Island	Espíritu Santo I.	Isabel Island	S
Percnon gibbesi		Cape San Lucas		S
Plagusia depressa tuberculata		Cape San Lucas		
Planes cyaneus	(San Francisco)	Santa Inez Bay	Escuinapa	
Sesarma sulcatum		Concepción Bay		S
GECARCINIDAE				
Cardisoma crassum		Agua Verde Bay		S
Gecarcinus planatus			San Ignacio Bay	S
Ucides occidentalis		Espíritu Santo I.		S
OCYPODIDAE				
Ocypode occidentalis	Todos Santos Bay	Carmen Island	Agiabampo	S
Uca brevifrons		Pichilinque Bay		S
Uca macrodactyla			Guaymas	S
Uca latimanus		La Paz		S
Uca mordax				
Uca musica	Santa María Bay	Pichilinque Bay	Tepoca Bay	S
Uca princeps	San Bartolomé Bay	Carmen Island	Ensenada de San Francisco	S
Uca reticulata	"West coast L.C."			

and Peru, for which transport by the Humboldt or Peruvian coastal current was postulated.

When it is considered that the tip of the peninsula of Baja California is effectively isolated from the opposite mainland by

deep water, and that there is no approach in the littoral for Panamic species except through the upper Gulf of California, which effectively filters them out, it is seen that for warm-water, littoral species the Cape San Lucas region is an island, and like all islands, subject to random arrival and dispersal. And just as there are brachyuran species common to Clarion and Galápagos (*Ebalia hancocki*), Clarion and Cocos (*Portunus brevimanus*), so should we expect to find species common to insular Cape San Lucas (as distinguished from the Gulf of California in its predominantly Panamic relationship) and these island outposts.

Once this is understood, the finding of the supposed Galápagos endemic *Leptodius cooksoni* first at Clarion Island, and more recently, in isolated colonies along the peninsular Gulf coast as far north as Puerto Escondido, becomes less surprising, while the range of *Parthenope triangula*, Cape region from Magdalena Bay to Puerto Escondido, Socorro, Clarion, and Galápagos Islands, and finally, La Plata Island, Ecuador, fits a pattern of random dispersal of the insular type. Furthermore, the fact that the 11 brachyuran species common to the Cape San Lucas region and the Galápagos Islands have no Atlantic analogues is a strong indication that they have never occurred in the Bay of Panama.

Summary

In the study just completed, Panamanian species intruding into the Gulf of California region (including (Magdalena Bay) numbered 131: cancroid crabs 47, grapsoid crabs 36, spider crabs 48. Species indigenous to the Gulf of California numbered 80: cancroid crabs 23, grapsoid crabs 32, spider crabs 25. Northern species numbered only 19: cancroid crabs 6, grapsoid crabs 5, spider crabs 8. To recapitulate, of a total of 230 species (cancroid crabs 76, grapsoid crabs 73, spider crabs 81), 131 species, or 57%, were Panamanian, 80 species, or 35%, were indigenous, and 19, or 8%, were northern.

When the above summary (see also Table IV) is compared with that of Glassell (1934), made just 25 years ago, it will be noted that the Panamanian segment has increased from 48 to 57% of the total, and that this has been at the expense of the indigenous element, which has declined from 40 to 34% of the total, and of the northern element, which has declined from 12 to 8% of the total. If the oxystomatous and allied crabs (Table V), 40 in number: 32 Panamic, 6 Gulf endemic, and 2 northern, omitted in order to make the above compilation more directly comparable to Glassell's, be included, the percentages become even more disparate: Panamanian 60%, indigenous 32%, northern 8%.

Further reflection reveals that the increment in the Panamanian sector has resulted, not so much from work done in the Gulf of California extending the range of Panamic species northward, as from work done in the Bay of Panama extending southward the range of species earlier known only from the Gulf of California. The smaller absolute number, as well as the lesser percentage, of northern species results in part from our inability to locate published records of their occurrence at Magdalena Bay or in the Gulf of California, presumably because these were known only to Glassell.

Conclusion

In concluding the presentation of distribution of Brachyura in the Gulf of California, it may be stated: (1) that the northern limit of the Panamic fauna in the Gulf of California cannot presently be defined because the dropping out of Panamic species is gradual and occurs throughout its entire length, with 50% of the Panamic species still present in its upper third; (2) that the southern limits of the warm-temperate fauna (the so-called "cold-water" species) may be defined by the ranges of the Gulf of California endemics

TABLE IV—A SUMMARY OF THE TOTAL NUMBER OF SPECIES IN THE THREE GROUPS

Cancroid crabs reported from Gulf of California	76 species
Grapsoid	73
Spider	81
Total of all species reported	230

The intrusion of Panamic species into the Gulf of California numbers 131 or 57% of the total. They are divided as follows:

Cancroid crabs	47 species, or	62%
Grapsoid crabs	36 ,	49
Spider crabs	48 ,	59
Total of the three groups	131 ,	57

(The above percentages represent the per cent which the Panamanian species bear to the total number of species in each family group.)

The number and percentages of species indigenous to the Gulf of California:

Cancroid crabs	23 species, or	30%
Grapsoid crabs	32 ,	42
Spider crabs	25 ,	31
Total of the three groups	80 ,	34

Northern intrusion of species in the Gulf of California:

Cancroid crabs	6 species, or	8%
Grapsoid crabs	5 ,	8
Spider crabs	8 ,	10
Total of the three groups	19 ,	8

A recapitulation of the foregoing tables:

Panamanian species in the Gulf	131 species, or	57%
Indigenous species	80 , or	35
Northern species	19 , or	8
	250 ,	100

and the southern California-northern Baja California coastal types occurring in the upper portion of the Gulf; and (3) that the Cape San Lucas "insular" region (Magdalena Bay to Puerto Escondido) supports a warm-water littoral fauna that is shared with the offshore islands of Socorro, Clarion, and Galápagos, and is independent of the mainland Panamic fauna of the Gulf.

Acknowledgment

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Addendum

The Scripps Institution of Oceanography Vermilion Sea Expedition with Robert H. Parker in charge of the biological phases of the investigation collected from 103 stations off Baja California and in the Gulf of California, March 2–May 20, 1959. Although ranging north of Angel de la Guarda Island, its chief contribution to faunistic studies was in the southeastern part of the Gulf, where a number of stations were occupied within the 100-fathom contour along the continental shelf, several to 800 fathoms on the continental slope, and one abyssal station in 1640 fathoms northwest of Tres Marias Islands. Only one brachyuran new to the Gulf fauna, *Ethusina faxonii*, resulted from the deeper haul, but new Gulf records may be reported for *Ethusina ciliatifrons* off Río San Lorenzo, 42–48 fathoms, *Mursia gaudichaudii* off Robelar, 48 fathoms, *Leiolambrus punctatissimus* off San Blas, 26 fathoms, *Cancer porteri* off Río San Lorenzo, 59–70 fathoms, and *Oediplax granulata* off Pta. Piaxtla, 24–26 fathoms. With the exception of the last, which is a Gulf of California endemic species with range extension southward, all are Panamic species with range extension northward.

TABLE V—PANAMIC SPECIES OF OXYSTOMATA AND ALLIED CRABS OCCURRING IN THE GULF OF CALIFORNIA: NORTHERN ADVANCE

	Peninsula, W side	*Peninsula, E side*	*Mainland side*	
RANINIDAE				
Raninoides benedicti		Willard Point		D
Raninoides ecuadorensis		Puerto Refugio		D
Ranilia fornicata	Santa María Bay	Carmen Island		D
DROMIIDAE				
Dromidia larraburei	(Monterey Bay)	Consag Rock	Rocky Point	S–D
Hypoconcha panamensis		Puerto Refugio	Rocky Point	D
Hypoconcha lowei		San Felipe	Rocky Point	D
Hypoconcha californiensis		San José Island		D
DYNOMENIDAE				
Dynomene ursula		Espíritu Santo I.	Tres Marías Ids.	S–D
DORIPPIDAE				
Ethusa mascarone americana		Consag Rock	Rocky Point	D
Ethusa mascarone panamensis			Isabel Island	S–D
Ethusa lata	San Roque Island	San Felipe	Tepoca Bay	D
Ethusa ciliatifrons			Río San Lorenzo	D
LEUCOSIIDAE				
Ebalia magdalenensis	Scammon Lagoon	Concepción Bay	Rocky Point	D
Lithadia cumingii	Magdalena Bay	Puerto Refugio	Georges Island	D
Speloeophorus digueti		Puerto Refugio	Rocky Point	D
Uhlias ellipticus		San José Island		S
Persephona edwardsii	Santa María Bay		Punta Piaxtla	D
Persephona subovata	Abreojos Point	Angel de la Guarda	Tiburon Island	D
Persephona townsendi		San Fermin Point	Cape Lobos	D
Leucosilia jurinei			Mazatlán	S
Randallia bulligera	San Diego	San José del Cabo	San Ignacio Bay	D
Randallia agaricias	Thurloe Bay	Cape San Lucas	Tres Marias Ids.	D
Iliacantha hancocki	Santa María Bay		San Ignacio Bay	D
Iliacantha schmitti	Point Tosco	Angel de la Guarda	San Pedro Nolasco	D
CALAPPIDAE				
Calappa convexa	Magdalena Bay	San Francisquito Bay	Rocky Point	S–D
Calappa saussurei	Point Tosco	Puerto Refugio	Ensenada de San Francisco	D
Mursia gaudichaudii	Farallones	Inner Gorda Bank	Off Robelar, Sin.	D
Cycloes bairdii	Santa María Bay	Los Frailes	Isabel Island	D
Hepatus kossmanni	Abreojos Point	Angeles Bay	Tiburon Island	D
Hepatella amica			Isabel Island	D
Osachila levis		Puerto Refugio	San Pedro Nolasco	D
Osachila lata			Tres Marías Ids.	D
HAPALOCARCINIDAE				
Hapalocarcinus marsupialis		Espíritu Santo I.		S

Cancer porteri may now be reported as a bi-temperate species that transgresses the tropics by submergence, being found in the Gulf of California, the Bay of Panama in 210 to 286 fathoms, and from Peru to Chile in the sublittoral.

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The Distribution and Affinities of the Marine Fish Fauna of the Gulf of California

BOYD W. WALKER

ALTHOUGH the fish fauna of the Gulf of California is clearly part of the Panamic fauna of the Eastern Tropical Pacific Region, it has certain peculiarities and distinctive elements which mark it with a character of its own. Beyond this, there are several areas within the Gulf with unique faunal peculiarities, which seem to have arisen in response to ecological factors. Although these areas are definitely different one from the other, they are not necessarily sharply delimited, and we know nothing about possible shifts in their ranges from year to year. It seems wiser at this time to treat them as areas with more or less distinct faunal assemblages, without attempting any sort of zoogeographic classification along a hierarchic system.

The region covered by this paper includes the entire Gulf of California, bounded on the south by Cabo San Lucas on the Baja California side, and by Topolobampo on the eastern or mainland side. Relatively little has been published on the fishes of this area. Most of the literature consists of lists of fishes collected at restricted localities and of descriptions of new species. Two checklists covering this region have appeared, but they were both merely uncritical literature compilations. The most valuable contributions have come from several recent group revisions (Briggs, 1955; Hubbs, 1952; Rosenblatt, 1959; and Springer, 1958). These papers have cleared up the problems of relationships in previously poorly understood groups, and the authors have discussed the zoogeographic implications of their findings. Unfortunately, all of the groups recently revised have consisted of fishes of rocky shores and of relatively shallow water. The authors reach reasonably uniform conclusions, but generalization on fish distribution cannot be attempted without consideration of the fishes from other habitats.

Even though literature records are scanty, there is a great amount of information available on the Gulf of California region in the form of as yet unreported, or only partially reported, collections. At the University of California, Los Angeles, we have 441 collections of fishes, comprising many thousands of specimens, from this area. This paper is largely based on these materials, and on the information gained on expeditions

made between 1949 and 1960, when these collections were made. Approximately 1000 collections of fishes have been made in the Gulf of California, but less than half of these have been recorded in the literature. For much of the following information I have drawn heavily on a manuscript list (Walker and Norris) of the fishes of the Gulf of California, based on the literature and all museum specimens known to us.

As can be seen from the above, the fish fauna of the Gulf of California is reasonably well sampled, certainly better than that of most marine areas in the world. A high proportion of the collections has been recently made, and modern methods have been used. Seines, trawls, dredges, and ichthyocides have been employed to sample much of the coastal area. There are still many miles of coastline which have not been touched, however, and more important, there remain many types of habitat which are as yet poorly sampled. I would estimate that the number of fishes recorded from the Gulf constitutes about 85 to 90% of the actual fauna, and that there are at least 20 or 30 new species not yet collected. There is little reason to think that the general conclusions reached here will be much changed by future finds, however. There is much to be learned of the details of distribution, and, in particular, of the controlling factors, but we now have sufficient information to see the general picture.

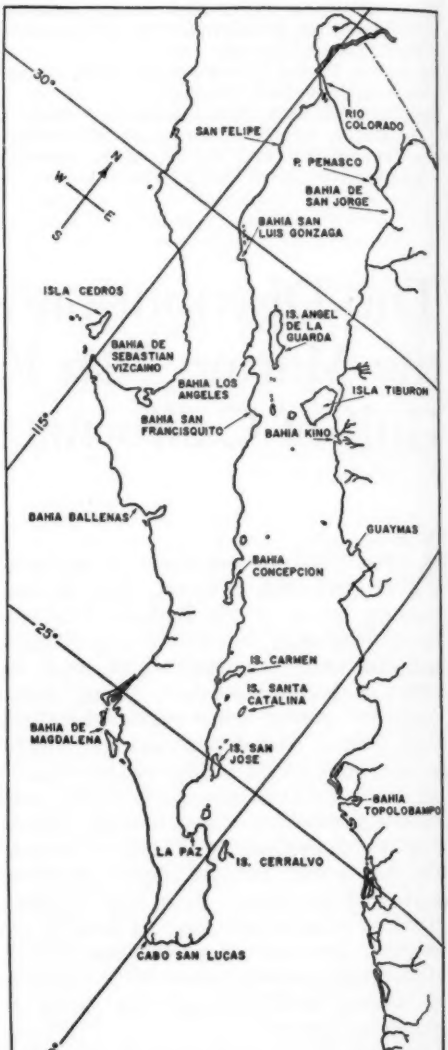

FIG. 1. Map of the Gulf of California, showing localities mentioned in the text.

Topography

The Gulf forms a long rectangle, about 680 miles long and 60 to 130 miles wide, which lies in a northwest-southeast direction. It is bounded by the peninsula of Baja California on the west, and by the Mexican states of Sonora and Sinaloa on the east. The shorelines on the two sides are quite different. The western side is characterized by rocky shores, often backed by high, rocky cliffs. Interspersed with the rocky headlands and numerous coves are sections of beach, usually short, but sometimes several miles long. There are numerous islands, with rugged, rocky shores. There are two major bays: Bahía

La Paz in the south and Bahía Concepción in the central portion. North of Bahía Concepción there is a transition to more sandy shore. Long, sandy beaches, broken by rocky headlands, run to about 40 miles north of Bahía San Luis Gonzaga. Between this point and the mouth of the Colorado River the sand beach is broken only by a rocky point at San Felipe and the mud banks of the Colorado delta area. The shelf is extremely narrow along most of this coast, but widens in the northern section above Isla Angel de la Guarda.

Sandy shores, broken in certain areas by rocky points, are more characteristic of the eastern shore. From the mouth of the Colorado a long, sandy beach runs southeastly to Puerto Peñasco, where there is a short section of low, rocky headland. South to Bahía Kino extensive beaches separate short, rocky stretches at the headlands. Between Bahía Kino and Guaymas lies a rocky scarp coast much like the typical coast of the western shore. Short beaches lie in coves between long stretches of rocky shores and cliffs. South of Guaymas there are sand beaches, almost unbroken until the rocky headlands at Mazatlán are reached. A rocky island lies just off Topolobampo, and some rocky islands occur inside the bay there, but these poor, rocky habitats are the only break in the sand, or sand and mud shores. The shelf is broad on the entire eastern shore, except along the rocky shore north of Guaymas. Mangroves line the shores of bays and esteros south of Bahía Concepción and Guaymas. North of these points the shorelines are virtually devoid of vegetation.

The lower end of the Gulf is rather sharply separated from the upper end by two large islands, Isla Angel de la Guarda and Isla Tiburon. In the lower end there is a considerable extent of deep water, and a number of basins separated from each other by transverse ridges. The deepest basins have a maximum depth of more than 3,000 meters, and a sill depth below 1,500 meters. In the upper Gulf there are shallower basins, with sill depths of 200 to 300 meters (Roden, 1958). Much of the upper Gulf is quite shallow and flat. The average depth is about 200 meters. A notable exception is a 1,000 meter deep trench between Baja California and Isla Angel de la Guarda.

Oceanographic Aspects

There has been relatively little oceanographic research done in the Gulf of California. What little is known has recently been summarized by Roden (1958) and by Roden and Groves (1959). The Gulf is the only evaporation basin in the Pacific Ocean. One of the outstanding features is the large annual range of sea surface temperatures. The range is greatest in the northern end; about 16°C. at Puerto Peñasco. Conditions are not so extreme in the southern portion, where the range is 9°C. at Cabo San Lucas. These pronounced seasonal variations occur in offshore regions as well as in the coastal areas. The seasonal variation of temperature extends down to a depth of about 200 meters; the average temperature in this depth ranges between 14°C. in winter to 18°C. in summer over most of the Gulf. A region of cold water occurs around Isla Angel de la Guarda and adjacent islands and points on the mainland. There is strong tidal mixing in this area.

There is little variation in salinity or oxygen in the Gulf, either geographically or annually, except at the mouths of rivers or in estero areas along the southeast shore. Here, variations from nearly fresh water to salinities considerably higher than sea water can be found in semi-isolated pools and lagoons at different seasons.

The tidal ranges vary considerably in the Gulf and are much greater in the northern portion than at the mouth. In the south the range of spring tides is about four feet, and the pattern varies only slightly in the entire Gulf south of Isla Tiburon. North of Tiburon the tidal amplitudes increase rapidly, reaching ex-

treme conditions near the mouth of the Colorado River, where spring ranges of 30 feet are found. Everywhere north of Tiburon the tide ranges are large, varying gradually from about nine feet to the great ranges in the north.

The current pattern is not yet well enough known to help the student of animal distribution in the solution to his problems. There is a general counterclockwise circulation, but the detailed current patterns are not known. We do know that strong tidal currents exist in the vicinity of Isla Tiburon and Isla Angel de la Guarda, and near the mouth of the Colorado River. Speeds of more than six knots have been reported (Roden and Groves, 1959). These currents are important not only as agents for animal distribution, but also because the mixing effected by them influences the ecology of large areas.

General Relations of the Fish Fauna

There is no doubt that the Gulf of California is part of the Tropical Eastern Pacific faunal region. This is clearly borne out by recent revisions of particular fish groups (Hubbs, 1952; Briggs, 1955; Springer, 1958; Rosenblatt, 1959) and was the conclusion of earlier workers (Gilbert and Starks, 1904; Meek and Hildebrand, 1928). Ekman (1953) treated it as such, but pointed out that it was a clearly distinguished faunal subregion. He based his conclusions on groups other than fishes.

In the Gulf, north of a line between Cabo San Lucas and Topolobampo, there are 586 species of fishes (Walker and Norris, MS). Of these, 60 are deep-water forms, and they will not be considered hereafter, since the distributional problems are quite different and distinct, and because the deep-water fauna has been only cursorily sampled. This leaves us with a total fauna of 526 species of fishes limited to the area of the continental shelf.

That the Gulf of California region has its faunal affinities with the eastern tropical Pacific area to the south is clearly borne out by a tally of the principal ranges of the fishes of the area. By principal range, I mean that range within which the fish is commonly found. I have eliminated those records which seem to be based on short term dispersal or on non-breeding populations. This action may seem to bias the data to the south, but in my opinion provides a clearer picture of faunal affinities for this type of analysis.

The principal range of two-thirds of the species (346 species) extends beyond the Gulf to the south. Most of these forms are found all the way to Panama or beyond. An additional 38 species are commonly found both north and south of the Gulf; many of these have their ranges centered to the south, however, and are best considered as Panamic elements with particularly wide distributions. Only 50 species range to the north exclusively, and well over half of these are found as disjuncts in the upper Gulf, as will be discussed later. The remaining 92 species have not yet been taken outside the Gulf, and must be considered as endemics. Summing up: 73% of the fish fauna consists of Panamic elements; 10% is of northern elements, most of which are of the San Diegan fauna; and 17% is endemic.

Barriers

The Gulf fauna is somewhat isolated from the Panamic fauna to the south by two barriers. These barriers are not equally effective for all parts of the fauna, and in reality are better considered as filter bridges. The two filters do not act in the same way, and this has caused subtle differences between the fauna of the west and east sides of the Gulf.

The long stretch of sandy shore, cut by many esteros, which lies between Guaymas and Mazatlán, has not been crossed by many rocky shore types. Most of the recent reviewers of fish groups confined to the rocky shore habitat have agreed that this area marks an important faunal break (Hubbs, 1952; Springer, 1958; Rosenblatt,

1959). Briggs (1955) found this break of little importance in the clingfishes, but it should be emphasized that the southern forms which have crossed this break are exceedingly rare in the north, and that there are five Gulf forms which do not range south of Guaymas on the eastern side of the Gulf. Four forms of chaenopsids are found from Guaymas northward, one from Mazatlán southward, and only one occurs at both localities (Stephens, MS). Three species of the brotulid genus *Ogilbia* are found at Guaymas but not at Mazatlán, one is found at Mazatlán but not north of that point, and there are no species in common (Walker, MS). Thus it seems apparent that this length of sandy shore marks the limits of the ranges of a large number of rocky shore fish species.

We must not infer that the lack of rocks is the only limiting factor in this area, however. Although data are meager, it is apparent that there are slight temperature differences between Guaymas and Mazatlán. Numerous sandy shore forms, such as *Sphyrna media* Springer, *Opisthopterus dovii* (Günther), *Pliosteostoma lutipinnis* (Jordan and Gilbert), *Anchoa arenicola* (Meek and Hildebrand), *Bagre pinnimaculatus* (Steindachner), several species each of the genera *Netuma* and *Galeichthys, Centropomus robalito* Jordan and Gilbert, and many other species, find their northern limit of range at various places in this area. The temperature differences evidently make this an area of rather gradual limitation of range of certain southern forms, and the lack of suitable habitat plus the temperature change produces a sharp break in the distribution of many rocky shore forms.

Some southern shore forms have evidently reached the Gulf by an alternate route. Thirty-seven species are found in the waters adjacent to Cabo San Lucas and from Mazatlán south, but not in the northern or eastern parts of the Gulf. These forms have almost certainly crossed the open ocean barrier across the mouth of the Gulf. The alternative route, that of moving northward along the east coast, crossing at the top, and then moving south on the west coast of the Gulf during a time when waters were warmer to the north, may be ruled out on two grounds. First, most of the species which are restricted to Cabo San Lucas and more southerly areas are rocky shore forms. We would not expect a selection for these types if they had followed the shorelines, because of the long stretches of sandy shore between Mazatlán and Guaymas, and again at the head of the Gulf. Actually the most noticeable lack in the Cabo San Lucas-La Paz region is in the catfishes and in the sciaenid genera *Ophioscion* and *Stellifer*. These sandy and muddy bottom groups are well represented in the region around Mazatlán, but are missing (except for one species of catfish) on the west side of the Gulf.

The idea that the disrupted distribution pattern was caused by warming and consequent expansion of the ranges of warm water forms throughout the Gulf, and subsequent cooling with restrictions of ranges to southern areas, is not compatible with the faunal pattern in the upper Gulf. Here we have a large representation of northern elements (to be discussed later) that are adapted to cooler temperatures. If the upper Gulf was warmed sufficiently to allow passage of southern elements subsequent to the establishment of the northern forms, these fishes, adapted to cooler waters, would almost certainly have been eliminated. The period of warming could have occurred prior to the establishment of the northern faunal element but this would mean that many elements of the Cabo San Lucas fauna have been isolated for a longer period of time than those in the upper Gulf. If they have been isolated longer we might reasonably expect that they would show a greater degree of differentiation from their parent stocks than do the northern forms, but, in fact, they show less. We can only assume, therefore, that the warm water dis-

junctions in the Cabo San Lucas area have become established after the northern element entered the upper Gulf, and that they must have crossed the open water barrier at the mouth of the Gulf to reach their present position.

On the outer coast of Baja California the Panamic fauna mixes in a rather complicated pattern with the San Diegan and Californian faunas (see the accompanying paper by Carl L. Hubbs). There seems to be a sharp break in the distribution of many forms at the temperature front just north of Cabo San Lucas (Roden, 1958), but collections are too few from much of the outer coast of Baja California for us to be sure of distributional details. It is clear, however, that many southern forms occur far to the north in localized areas of warmer water. A considerable number of these forms are found elsewhere only in the Gulf of California, and are endemic to the Gulf and outer Baja California coast.

Distinctive Elements of the Gulf Fauna

The fish fauna of the Gulf of California, although certainly comprising a part of the Panamic fauna, has certain distinctive elements. As contrasted to the rest of the Panamic fauna, the Gulf fauna has an unusually high number of rocky shore species, a relatively poor representation of muddy bottom forms, and a rather high percentage of endemic species (17%).

The richness of the rocky shore fauna is best exemplified by an analysis of those groups which have been recently revised. By confining ourselves to these groups we can be certain of accurate and fairly complete taxonomic treatment. The taxonomy of many of the speciose rocky shore groups, such as the muraenids, pomacentrids, labrids, eleotrids, and the gobiids, is still too poorly known for us to draw reasonably valid conclusions as to the distribution of their member species.

In most cases the representation of rocky shore species in the Gulf is far richer than it is for any like latitudinal range in the rest of the eastern tropical Pacific mainland, or more striking yet, for any equal length of shoreline. Of the eight mainland species of the clinid genus *Malacoctenus*, six species are found in the Gulf of California. No more than five are found in any similar stretch of coast to the south, and over most of the coastline four or fewer are present (Springer, 1958). In the closely related genus, *Labrisomus*, three of the five mainland eastern tropical Pacific species are found in the Gulf. Only at Mazatlán is a like number found, and to the south only two species are found in a comparable area (Hubbs, 1952). *Paraclinus*, another clinid genus, has only four species in the eastern tropical Pacific, but two of these are common in the Gulf of California, and the range of a third bypasses the Gulf, and will almost certainly be found to include the Gulf (Hubbs, 1952). There are nine species of the blennioid family Tripterygiidae on the mainland of the eastern tropical Pacific. Five of these species occur in the Gulf of California, and three of these are endemic. There are also five species found along the Mexican mainland south of the Gulf, and of these two are endemic, but only three species range south of this area (Rosenblatt, 1959). In another blennioid family, the Chaenopsidae, there are 17 eastern Pacific species. Eleven of these are found in the Gulf of California, and only ten species have been taken to the south (Stephens, MS). It seems clear from the account above that there is a particularly rich blennioid fauna in the Gulf of California. The blennioids constitute one of the most speciose groups of rocky shore fishes.

The only other large group of rocky shore fishes which has been adequately reviewed is the order Gobiesociformes, the clingfishes (Briggs, 1955). There are 19 species on the mainland of the eastern tropical Pacific, and ten of these occur in the Gulf of California. Five species are endemic in the Gulf. Nine species are found on the Mexican mainland south of the Gulf, and eight species are found in

the region of Costa Rica and Panama. While the Gulf gobiesocid fauna is not as strikingly rich as the blennioid fauna, it is certainly well developed and strongly represented. All the present evidence indicates that the other groups of rocky shore fishes will show this same pattern of particularly strong representation in the Gulf of California.

In contrast, certain fishes usually found over sandy and muddy bottom types are poorly represented. Gilbert and Starks (1904) stated that the Gulf of California fauna differed principally from that of the region to the south in the lack of sciaenids and ariids. A great deal of intensive collecting has been done since this statement was made and the difference is still apparent. Mazatlán is the northern limit of distribution of seven species of sciaenids, and an additional seven species extend northward only to the mouth of the Río Mayo or to San Juan Lagoon south of Guaymas. Only 22 species occur in the rest of the Gulf, including the east shore north of Guaymas and the entire western side. The sciaenid fauna on the west coast of Panama consists of 42 species, and includes several genera which are not found in the waters of the Gulf. The ariids, or catfishes, are very poorly represented. Only eight species are known to occur north of Mazatlán, in contrast to 21 species known from the Pacific waters of Panama. The catfishes in the Gulf are largely confined to the eastern shore south of Guaymas. Only one species, *Bagre panamensis*, is found on the western shore of the Gulf.

Other families that are largely restricted to the sand and mud bottom habitat are relatively better represented, but in almost all cases there are fewer species in the Gulf than in the waters to the south. The families Clupeidae, Engraulididae, Centropomidae, and Haemulidae all show this trend in varying degrees.

Although endemic species are numerous in the Gulf, there are only four endemic genera, all monotypic. This scarcity of distinctive genera indicates that the Gulf fauna has developed in relatively recent times.

Distinctive Areas Within the Gulf

Within the Gulf there are several more or less distinct faunal assemblages. The areas in which these different assemblages occur correspond closely to the areas of principal differences in ecological situations. As has been pointed out, however, most of the oceanographic data is extremely sketchy, and it remains for future work to establish exact relationship between distribution patterns and ecological data.

Within the Gulf of California we can distinguish four faunal areas: the upper Gulf, which extends north of a line from Bahía San Francisquito past the southern tip of Isla Tiburon; one that we shall refer to as the central Gulf, which includes the short length of shoreline from Bahía Kino to Guaymas on the east side of the Gulf, and the much longer shoreline between Bahía San Francisquito and La Paz; the Cabo San Lucas area, which extends north from the cape to the vicinity of La Paz; and the southeastern Gulf, which includes the low, estero-broken shoreline south of Guaymas.

Of these, the fauna of the southeastern Gulf is the least distinctive. Indeed, if we were trying to establish natural faunal areas with distinct boundaries, this area should be included with that extending to the south. Its main point of distinctiveness is that it has a very poor rocky shore fauna because of the almost complete lack of proper habitats, and that many of the sand and mud bottom forms find their northern limit of distribution near its northern boundary. The ranges of only several of those species here considered as Gulf endemics extend into this region.

The faunas of the other areas within the Gulf are more clearly differentiated from the rest of the Panamic fauna. Within these areas there are 92 endemic species, and it is here that the marked lack in sandy and muddy bottom forms

and the rich representation of rocky shore forms is apparent.

Of the endemics, 37 range widely through the Gulf area, 22 species are confined to the upper Gulf, 27 species are found only in the southern sections, and six species are found only in the vicinity of Cabo San Lucas. Almost all of the species indigenous to the upper Gulf are found only in waters of moderate depths (about 15 to 300 feet). In sharp contrast, most of the species endemic to the southern areas are restricted to intertidal and shallow waters.

The upper Gulf is characterized by a relatively depauperate fauna, with a strong element of endemics from the zone of moderate depths, and a large number of disjunct species from more northern areas of the outer Pacific Coast.

Only 259 species of fishes have so far been taken in the upper Gulf area, in contrast to the 504 species known from the lower areas. Although we cannot be certain as to the reasons for this drastic reduction in total fauna, it seems reasonable to assume, for the present, that the fauna is restricted by two ecological factors which change rather abruptly in this region. The great annual range in temperature is probably the most important factor. As described earlier, the upper Gulf is both warmer in the summer and colder in the winter than the lower Gulf areas. It seems probable that the colder winter temperatures exert the greatest limiting effect, since most of the forms are of southern affinities. The extreme range of annual temperatures may itself act as a limiting factor, however. The sudden change in tidal range in the upper Gulf seems also to act as a limiting factor. The restriction in intertidal and rocky, subtidal species is especially noticeable, and may well be due in part to the extreme tidal fluctuations.

The ecological factors mentioned above are probably also responsible for the development of numerous endemics from moderate depths and the extremely limited number of shallow water endemics. The three shallow water endemics, *Gilichthys seta* (Ginsburg), *Ilypnus luculentus* (Ginsburg), and an undescribed species of *Ilypnus,* are all closely related gobies from a muddy or sandy bottom habitat. No rocky shore, shallow water species are strictly endemic to the upper Gulf, but two forms, *Tomicodon humeralis* (Gilbert), a clingfish, and *Malacoctenus gigas* Springer, a clinid, have their principal range there. *Tomicodon humeralis* is restricted to the upper Gulf, except that it is occasionally taken as far south as Guaymas on the east side of the Gulf. *Malococtenus gigas* is somewhat more common to the south, but it is never dominant there. In the northern Gulf *M. gigas* is by far the most common clinid. Nineteen endemic species from moderate depths are found, including three sciaenids, three ophidiids, and the remainder from various spiny-rayed families. No sharks or soft-rayed fishes are endemic to the upper Gulf.

A particularly striking element of the northern Gulf fauna is composed of fishes common on the outer Baja California and southern California coasts, but absent in the extreme southern Gulf. Some of these disjuncts are extremely common in the upper Gulf, and they constitute an important segment of the fauna. Many of them show varying degrees of differentiation from the outer coast forms, but in most cases the differences are slight, and often are limited to color variations. Nine species are restricted to the northern area in the Gulf: *Cetorhinus maximus* (Gunnerus), *Triakis semifasciata* Girard, *Raja inornata* Jordan and Gilbert, *Myliobatis californicus* Gill, *Xystreurys liolepis* Jordan and Gilbert, *Anisotremus davidsoni* (Steindachner), *Cynoscion nobilis* (Ayres), *Scorpaena guttata guadalupae* Fowler, and *Stereolepis gigas* Ayres. Several of these are notably large species. *Cetorhinus maximus,* found world-wide in temperate and subarctic seas, commonly reaches a length of 30 feet. *Stereolepis*

gigas, the distinctive giant sea bass of the Californian and San Diegan faunas, reaches weights of 500 to 600 pounds. *Myliobatis californicus* and *Cynoscion nobilis* commonly reach 50 pounds in weight, and *Triakis semifasciata* may reach five feet in length.

Thirteen northern species are found in abundance in the upper Gulf, and occur less commonly or are rare in the more southern areas. They are: *Heterodontus francisci* (Girard), *Squatina californica* Ayres, *Sardinops caerulea* (Girard), *Hippoglossina stomata* Eigenmann, *Hypsopsetta guttulata* (Girard), *Pleuronichthys verticalis* Jordan and Gilbert, *Cheilotrema saturnum* (Girard), *Umbrina roncador* Jordan and Gilbert, *Pimelometopon pulchrum* (Ayres), *Gillichthys mirabilis* Cooper, *Quietula y-cauda* (Jenkins and Evermann), *Ilypnus gilberti* (Eigenmann and Eigenmann), and *Hypsoblennius gentilis* (Girard).

The genera *Leuresthes* and *Girella*, with endemic species in the San Diegan fauna, are represented by closely related species in the Gulf. The Gulf forms, *Leuresthes sardina* (Breder) and *Girella simplicidens* Osburn and Nichols, are exceedingly common in the upper Gulf, but become uncommon in the central area, and are absent south of Guaymas and Isla Carmen. All of the above species have their principal range in the upper Gulf, and are characteristic of that area.

Just how and when the northern faunal element reached its present position in the upper Gulf is still a question. It may have moved around the present peninsula, or there may have been a movement through an oceanic connection which existed in the region of the La Paz plain during the late Pleistocene (Beal, 1948). If passage was effected through an isthmus in the La Paz region, only a slight general cooling of the waters of the Gulf would have been necessary to allow the influx of the colder water forms from the waters of the outer coast. A much more extensive cooling would seem to be required to allow movement around the cape, because of the temperature front which exists in this region. The high degree of endemism of warm water types in the southern Gulf does not seem to be compatible with any theory involving extensive cooling in the Gulf region. On the other hand, the small degree of differentiation of many of the disjuncts in the upper Gulf would seem to indicate that they have been separated from their parent stocks for a relatively short time. A significant group of warm water disjuncts in the Cabo San Lucas area show even less differentiation from their parent stocks, however, and must have arrived at their present location after the upper Gulf fauna was established. It seems most probable, therefore, that most of the northern disjuncts reached the Gulf through a late Pleistocene seaway in the La Paz region, at a time when water temperatures in the Gulf were slightly cooler than at present. It is not impossible, however, that some forms have circled the present cape region. Some of the larger species, such as *Cetorhinus maximus*, *Stereolepis gigas*, and *Myliobatis californicus*, might conceivably be able to traverse this route under present day conditions.

The fauna of the central Gulf is characterized primarily by those features discussed for the Gulf as a whole. There are a reasonably rich fauna, with particular development of the rocky shore elements, a somewhat restricted sandy and muddy bottom fauna, a considerable endemism, and a noticeable group of forms having their principal ranges to the north. These are the general characteristics of the fauna of the Gulf of California, and the central Gulf might be considered as the "typical" area. The other areas differ from it largely in the particular development or lack of development of one of the above mentioned characteristics.

Well over half of the 27 endemics of the central Gulf area are species of shallow water and rocky shores. The majority of

the 37 endemics found in both the upper and central Gulf areas is also from this type of habitat. In the central Gulf area the tidal ranges are not great, and temperature conditions are much closer to those found farther south. The prevalence of rocky shores, temperature conditions somewhat more extreme than those to the south, and the presence of a least partial barriers for rocky shore fishes, probably are responsible for the relatively high degree of endemism for rocky habitat types.

The fauna of the Cabo San Lucas area bears some remarkable similarities to an insular fauna. These similarities, plus an almost complete lack of northern elements, several endemics, and a large group of species found only in this region and on the mainland at Mazatlán and southward, set this area apart from the rest of the Gulf.

There is an unusually high number of western Pacific forms in the cape region. Particularly significant are the records of species for which the Cabo San Lucas area is the only eastern Pacific mainland record. These include: *Echidna zebra* (Shaw), *Priacanthus cruentatus* (Lacépède), *Caranx stellatus* Eydoux and Souleyet, *Thalassoma lutescens* (Lay and Bennett), *Iniistius pavoninus* (Cuvier and Valenciennes), and *Acanthurus triostegus* (Linnaeus). These forms are common on certain eastern Pacific oceanic islands, and are conspicuous island elements. In addition, *Xyrichthys mundiceps* Gill, long considered an endemic of Cabo San Lucas, is extremely close to an Hawaiian form, if not conspecific with it. A juvenile *Xyrichthys* has recently been taken on Clipperton Island by Mr. Wayne Baldwin.

The northern element, so characteristic of the upper Gulf and present in significant numbers in the central Gulf, is noticeably lacking in the Cabo San Lucas area, where the faunal affinities are almost entirely to the south. Thirty-seven species with a primary range extending from Mazatlán southward occur in the Gulf of California only in the Cabo San Lucas area. Most of these are forms frequenting rocky shores, and many different families are represented. Typical forms include *Apogon parri* Breder, *Rhegma thaumasium* Gilbert, *Pomacentrus flavilatus* Gill, *Cirrhithichthys corallicola* Tee-Van, *Entomacrodus chiostictus* (Jordan and Gilbert), *Malacoctenus zonifer zonifer* (Jordan and Gilbert), *Enneanectes sexmaculatus* (Fowler), *Tomicodon myersi* Briggs, and *Prionurus punctatus* Gill. Species from other habitats are fewer, but diverse type of habitats are represented, as indicated by the presence of *Strongylura fodiator* (Jordan and Gilbert), *Sphagebranchus selachops* (Jordan and Gilbert), *Seriola colburni* (Evermann and Clark), *Rabirubia inermis* (Peters), and *Umbrina dorsalis* Gill.

Collections are not yet complete enough to determine just where the fauna of the Cabo San Lucas area merges into that of the central Gulf. It seems probable that it is some place between Isla Cerralvo and La Paz, but exact information is wanting. There are also few data to indicate why so many forms should be limited to this small area. Water temperature almost certainly plays a large part. Hard coral is extremely rare in the eastern tropical Pacific, but it is found in the Cabo San Lucas area. Several deep canyons also meet the shore in this area, and these may in some way influence the insular appearance of the fauna.

Summary

The fish fauna of the Gulf of California is clearly part of the Panamic fauna, but it has certain peculiarities and distinctive elements which characterize it. Seventy-three per cent of the fish fauna of the Gulf consists of Panamic elements, 10% is of northern elements, and 17% is endemic. As compared to the region to the south, there is an unusually high number of rocky shore species, and a relatively poor representation of those forms that live on mud or mud and sand.

Although endemic species are numerous, there are only four endemic genera, all monotypic.

The Gulf fauna is somewhat isolated from the Panamic fauna to the south by two barriers: the long stretch of sandy shore between Guaymas, Sonora, Mexico, and Mazatlán, Sinaloa, Mexico, tends to limit the distribution of many rocky shore forms; and the open water between the mainland and Cabo San Lucas has prevented the passage of certain warm water forms to the peninsula.

Within the Gulf there are several more or less distinct faunal assemblages. The areas in which these different assemblages occur correspond closely to the areas of principal differences in ecological situations. The fauna of the southeastern Gulf, south of Guaymas, is like that of the coastline to the south. The upper Gulf, north of a line from Bahía San Francisquito past the southern tip of Isla Tiburon, is characterized by a relatively depauperate fauna, with a strong development of endemic species from moderate depths, and a large number of disjunct forms from more northern areas of the outer Pacific Coast. The central Gulf includes the short length of shoreline from Bahía Kino to Guaymas on the east, and the much longer shoreline between Bahía San Francisquito and La Paz on the west. The central Gulf fauna shows the general characteristics of the Gulf, and has a strong element of shallow water endemics. The Cabo San Lucas area extends north from the cape to the vicinity of La Paz, and the fauna is characterized by the presence of a group of western Pacific species found elsewhere in the eastern Pacific only on oceanic islands, a complete lack of northern elements, several endemics, and a large group of species found only in this area and on the mainland at Mazatlán and southward.

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The Marine Vertebrates of the Outer Coast[1]

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IT IS ONLY a first, in fact a very crude approximation, to include the Gulf coast of Baja California and the tip of the peninsula in the tropical Panamic Province and the rest of the outer coast in the warm-temperate (San Diegan) division of the Californian Province. The faunal changes along the outer coast of Baja California, in particular, are neither so abrupt nor so regular as to justify drawing definite boundaries to such provinces. The facts of the distribution of life along this coast emphasize the serious doubts that may be entertained regarding the wisdom of attempting a definite areal zoogeographic classification along an hierarchic system. It may well be more meaningful and dynamic to treat each areal faunal assemblage as a complex of faunal elements of diverse provenance, as Mayr (1946) and Parkes (1958) have done for the birds of North America.

General Distributional Pattern

The marine vertebrates of the outer coast of the Baja California peninsula—the prime subject of this paper—change irregularly from almost strictly tropical (Panamic) at Cabo San Lucas to largely warm-temperate (San Diegan) just north of the political boundary between Baja California Norte and California.

Though basically tropical, the marine vertebrate fauna of the Cape region lacks many of the species characteristic of the Central American coasts, and includes a number of San Diegan types, such as the California yellowtail, *Seriola dorsalis* (Gill), which also occurs in the Gulf, and the opaleye, *Girella nigricans* (Ayres), which is represented by a cognate species in the Gulf. Another San Diegan type, which occurs in shallower water to the northward, on both sides of the peninsula, namely the sheephead, *Pimelometopon pulchrum* (Ayres), rounds the Cape in relatively deep water. Included also are a number of Indo-Pacific fishes, including the Moorish idol, *Zanclus cornutus* (Linnaeus). In fact, as a result of recent explorations, Boyd W. Walker and Richard H. Rosenblatt regard the fauna of the Cape region as having insular characteristics. Indeed, it is very probable that the Cape mountains at no very great geological antiquity did constitute an island mass.

In conformity with the oceanographic conditions (Roden, 1958; Roden and Groves, 1959), the tropical elements in the Cape fauna extend much farther northward, and dominate the fauna much farther, on the Gulf side of the peninsula than on the ocean-exposed western shore. Along the western coast the marine vertebrate fauna, like the surface temperature, changes abruptly between the Cape and the region about Bahía Magdalena. The alteration in the fauna is most abrupt along the open coast, where the coastal water is subject to upwelling. Cooling of the shore water by upwelling is apparent as far south at least as the region of Cabo San Lázaro, near the offing of Bahía Magdalena. In this region of upwelling such typical Californian intertidal fishes as *Clinocottus analis* (Girard) and *Gibbonsia elegans* (Cooper) reach their southern limit.

[1] Contributions from the Scripps Institution of Oceanography, New Series.

Within the Bahía Magdalena complex, where the waters are less affected by upwelling and are more subject to insolation, and are hence warmer, a more tropical fauna persists. This is especially true of Bahía Almejas, the warm, shallow, southern extension of Bahía Magdalena, in which the anchoveta, *Cetengraulis mysticetus* (Günther), finds its northernmost locality of abundance.

Farther north, in the lagoons and largely enclosed bays, and in the gentler coastal recesses (bahías Sebastián Vizcaíno and Todos Santos), the fauna also remains more nearly tropical than along the intervening coasts, where upwelling dominates insolation. In the enclosed waters tropical fishes occur incongruously far northward. Surveys are incomplete, but conspicuous examples among the fishes have come to light. To mention a few: *Ophioblennius* occurs in Bahía Tortuga; *Pareques viola* (Gilbert) and representatives of tropical blennioid genera (*Malacoctenus, Labrisomus, Enneanectes,* and *Ogilbia*) in the very warm southern shore of Bahía Sebastián Vizcaíno (Dawson, 1952); *Exerpes* in Bahía Tortuga and in Scammon and San Ignacio lagoons (Hubbs, 1952: 94–95); the tropical goby genus *Microgobius* also in Laguna San Ignacio; and *Cynoscion parvipinnis* Ayres in Bahía Todos Santos. Obviously, it would violate the facts either for the upwelling waters of the outer coast or for the insolated waters of the bays and lagoons to draw a faunal boundary line at any one latitude along the western coast of Baja California.

The temperature surveys now in progress, expanding the pioneering work by McEwen (1916) (see reports by Dawson, 1945–1953, his paper in this symposium, and preliminary statements by Hubbs, 1948, 1959a), offer a ready explanation for the incongruity between the biotic affinities along the open coast and in the bays and lagoons. Great discrepancies exist between the surface temperatures in these habitats during the warmer months (the temperatures are more uniform during the colder months). The conservative water masses of the lagoons and enclosed bays become warmed by insolation. The open "bays" (Sebastián Vizcaíno and Todos Santos) receive inflowing currents that tend to elevate the surface level, and hence inhibit upwelling, because they open to the northwest and are enclosed on the northeast, east, south, and, in part, on the southwest. Not only the prevailing northwesterly winds, but nearly all northerly and westerly winds induce flow into the open bays. Along the open coast, which generally trends from northwest to southeast, most winds, ranging from westerly through northerly to easterly, supplemented by Corioli's force, induce movement of the surface water away from the shore, to be replaced by cooler water from below. The upwelling and cooling is particularly striking on the southern and southwestern, and occasionally southeastern, sides of points, where one can actually watch the surface waters move offshore, when brisk winds, sweeping down the coastal slopes, induce catspaws that flick seaward. The surface temperatures on the northern and southern sides of points usually contrast sharply during the warmer months. The greatest contrasts have been observed at Punta Banda, which forms the southern border of Bahía Todos Santos. Here, at stations only two miles apart (across the base of the point), the surface temperatures along the coast have differed by as much as 12° C, commonly by 3° to 9° C. On the rare occasions when the temperature in summer is higher on the southern side of a point, the wind is from a southern sector, piling water up on the south side and driving it out on the north side.

The shallow-water fishes, along with the littoral algae (Dawson, 1945–1953) and the invertebrates (see the paper in this symposium by Garth), reflect the irregular temperature differentials. Dawson has documented the evidence extensively, and I have been accumulating physical

and faunal data since 1945, with monthly temperature surveys since 1948. The whole aspect of the inshore fish fauna in the areas of strong upwelling along the northwestern coast of Baja California is reminiscent of that in the region of Monterey, California, where there is also much upwelling, inducing temperatures far below those in southern California. Some northern fishes, including the intertidal genera (or subgenera) *Amphigonopterus, Allocottus,* and *Epigeichthys,* occur disjunctly in areas of intense upwelling in Baja California, as about Puerto Santo Tomás, after skipping the warm waters of the southern part of southern California. The names of these species in different systematic appraisal are: *Amphigonopterus* (or *Micrometrus*) *aurora* (Jordan and Gilbert), *Allocottus* (or *Clinocottus*) *embryum* (Jordan and Starks), and *Epigeichthys* (or *Xiphister*) *atropurpureus* (Kittlitz). Another fish that seems to skip southern California south of the northern Channel Islands, to occur in the upwelling area of Baja California, is *Cebidichthys violaceus* (Girard) (the record from Point Loma, California, by Hubbs and Barnhart, 1944, proves to have been based on an unnamed genus and species). Other inshore species that are rare in the warm waters of southern California, but commoner on either side, are *Artedius lateralis* (Girard) and *Artedius notospilotus* Girard.

Nearly all northern fishes that reach as far south as San Diego, California, have by now been recorded, or have been taken by us, in the cooler waters of northwestern Baja California. The same relation holds for other marine vertebrates (as also for algae and invertebrates). Thus, I have found the black scoter, *Oidemia nigra americana* Swainson, and the rock sandpiper, *Erolia ptilocnemis* (Coues), in northwestern Baja California (Hubbs, 1955, 1956, 1960), and I have seen in waters off that coast two northern sea mammals long thought not to occur south of California, namely the northern fur seal, *Callorhinus ursinus* (Linnaeus), and the Dall porpoise, *Phocoenoides dalli* (True). It will probably prove to be a general rule, for all groups of littoral organisms, that the biota of northwestern Baja California includes the northern types that penetrate into the relatively warm water in the region of San Diego, California, plus a few species that skip those warm waters.

Other fishes (and invertebrates), which range continuously from the cold waters north of Point Conception through southern California to the upwelling areas of Baja California, follow a more or less isothermal path by submerging to greater depths in southern California and then coming into shallower water again in Baja California. Thus, species of *Sebastodes* that occupy depths of 30 to 80 meters about San Diego occur at about 10 to 30 meters near Santo Tomás. Species that occur between tides in central California but infratidally in southern California, such as *Sebastodes chrysomelas* (Jordan and Gilbert) and *Liparis mucosus* Ayres, reappear between tides in Baja California. This is no doubt a general phenomenon, which is illustrated among invertebrates by the red abalone, *Haliotis rufescens* Swainson, and by the large sea urchin, *Strongylocentrotus franciscanus* (Agassiz). Similarly, the whole community of the giant kelp, *Macrocystis,* extends into the shore rocks in central California and in the upwelling areas of Baja California, but near San Diego grows in about 10 to 30 meters of water.

The present pattern in the distribution of temperatures and of organisms along the outer coast of Baja California appears from recently gathered evidence to be of long standing, though modified by marked latitudinal shifts. Such shifts were no doubt accentuated during the Pleistocene. It was probably during the periods of continental ice sheets—the last ending about 10,000 years ago—that the ocean waters of the tropical eastern Pacific were sufficiently cooled to allow the transgres-

sion of the equator by such now antitropical organisms (species or species groups) as now approach or barely reach the limits of the tropical fauna—in the Cabo San Lucas region from the north and in Peru from the south (Hubbs, 1952). Among the vertebrates, cognate pairs now flanking the tropics on either side include various sharks, and teleosts referred to the genera *Sardinops, Engraulis, Xenistius, Sebastodes* (the *rosaceus* species group only), and *Agonopsis;* also marine mammals of the pinniped genera *Mirounga, Zalophus,* and *Arctocephalus* (of the group *Arctophoca,* embracing the species *philippii* and *townsendi*) and the cetacean genera *Phocoena* and *Berardius.* Some marine birds may also be involved, as are also various invertebrates and a few algae, particularly the giant kelp, *Macrocystis.*

It may be assumed: (1) that the warm-temperate (San Diegan) and cool-temperate (Montereyan) vertebrate faunas were displaced southward, as the invertebrate faunas surely were, during the Wisconsin and earlier ice periods; (2) that some cool-temperate species were displaced so far southward that they were able to round Cabo San Lucas, where the tropical waters now interpose a barrier for such forms; (3) that anadromous trout then reached streams of western Mexico on the east side of Golfo de California; and (4) that the Gulf became populated by various organisms now characteristic of the fauna of southern California and northwestern Baja California. Some of these San Diegan types have survived in the Gulf, despite the high summer temperatures, probably because the cool winter temperatures (Roden, 1958; Roden and Groves, 1959) provide tolerable conditions for spawning and early development. They are thus able to survive alongside tropical forms that tolerate the cool winter temperatures (such types of temperature tolerance were discussed by Hutchins, 1947). The California spiny lobster, *Panulirus interruptus* (Randall), is a fine example among the invertebrates, along with several crabs that are being treated in a companion paper by John S. Garth. Among fishes in this category are representatives of the genera *Cetorhinus, Urolophus, Gymnura, Paralichthys, Hypsopsetta, Pleuronichthys, Xystreurys, Paralabrax* (*maculatofasciatus*), *Atherinops, Leuresthes, Anisotremus, Cheilotrema* (and probably other sciaenids), *Girella, Sebastodes, Gillichthys, Quietula, Ilypnus, Syngnathus,* and *Porichthys.* As a whole, these types are absent or very scarce in the Cape region. They are trapped in Golfo de California, just as many Pleistocene relicts are trapped in the geographically and zoogeographically analogous Gulf of Mexico (Hedgpeth, 1953). As in the Gulf of Mexico, many of the Pleistocene relicts in Golfo de California have undergone varying degrees of differentiation during their isolation.

During interglacial times the vertebrate fauna of the Baja California outer coast was no doubt displaced northward, but little evidence of such displacement can be cited. Some of the most tropical elements in the bays may be interglacial relicts, but they may merely be populations derived from immigrants that ranged northward in recent warm years. There is some paleontological evidence of northward dispersals during the Pleistocene. Perhaps the most spectacular example is that of a subtropical fauna, seemingly of Pleistocene age, that I have discovered on Guadalupe Island, and am analyzing with the collaboration of Emery P. Chace and others. This presumably interglacial fauna comprises a mixture of San Diegan species with a reef-building coral and with various mollusks that are now characteristic of the Panamic Province.

About 100 years ago the ocean temperatures of northwestern Baja California were no doubt sufficiently warmed to have allowed the transgression of this upwelling area by the tropical and subtropical

types that then occurred at San Diego, California, but that are now wholly or largely confined to more southern waters, in Baja California Sur, and southward (Hubbs, 1948). Fishes illustrating this type of distribution include:

Anchoviella miarcha (Jordan and Gilbert) (see Hubbs, 1953).
Chaetodon humeralis Günther (see Hubbs and Rechnitzer, 1958).
Chaetodipterus zonatus (Girard).
Eucinostomus argenteus Baird and Girard.
Caranx caballus Günther.
Dermatostethus punctipinnis Gill (known only from the original description, but doubtless of southern origin).
Hippocampus ingens Girard.
Sphoeroides annulatus (Jenyns).

Other fishes of southern origin, which were reported from California in 1880, may have been holdovers from this warm period. This northward dispersal about the middle of the last century extended as far north as Monterey, California, where San Diegan types were encountered (Hubbs, 1948). Meteorological data confirmed the faunal indications of warmer temperatures at San Diego and at Monterey, with a decline until the early years of the twentieth century. There are indications that various other animals ranged farther north 100 years ago. In this connection we may list a clam, *Laevicardium elatum* (Sowerby), a crustacean, *Pleuroncodes planipes* Stimpson, and a porpoise, *Tursiops gillii* Dall.

Currently, in warm years, such as 1957 through 1959, the cold barrier of northwestern Baja California has been sufficiently weakened to have allowed the incursion into southern California, or even into more northern regions, of fishes that ordinarily live only farther south; or to induce in northern Baja California and in southern California a great increase in the numbers of types that are common southward, such as the yellowtail, *Seriola dorsalis* (Gill), the dolphinfish, *Coryphaena hippurus* Linnaeus, and the bonito, *Sarda lineolata* (Girard). The fish evidence for 1957–1959 is being reviewed by John Radovich. The northward movement of southern types in these warm years across and beyond the northwestern coast of Baja California involves not only fishes, which seem to be remarkably reactive to temperature changes, but also other marine vertebrates, such as the sea turtles *Chelonia, Caretta,* and *Lepidochelys;* also tropical seabirds, such as the red-billed tropicbird, *Phaethon aethereus mesonauta* Peters, and the magnificent frigatebird, *Fregata magnificens rothschildi* Mathews, and even the skua, *Catharacta skua* Brünnich (Small, 1959), which has not yet been reported from Mexico. Various marine invertebrates, including *Pleuroncodes planipes,* also moved northward in the warm period of 1957–1959, reappearing in numbers in Monterey Bay for the first time in decades.

The bathybial demersal fauna of the continental slope off Baja California is yielding a number of fishes, such as the hagfish, *Myxine circifrons* Garman, and the hake, *Merluccius angustimanus* Garman, that also occur in deep water off Panama and that exemplify, along with species of other genera, including *Lycodes,* the submergence in the tropics of types that occur antitropically in shallower water. Other bathybial bottom fishes of western Baja California, like the littoral fishes, are of either southern or northern origin.

The bathypelagic fish fauna off Baja California is yielding a considerable assortment of tropical forms that are presumably carried northward by a deeplying current that is under study by Joseph L. Reid, Jr. Included among these are some of the bizarre genera of the black mid-depths, such as *Derichthys, Saccopharynx, Dysalotus, Kali,* and *Gigantactis.*

The epipelagic and the shallower bathypelagic fish faunas along the peninsula exhibit changes with latitude that somewhat parallel the changes in the littoral fauna. These changes involve geminate pairs as well as altered assemblages.

Endemism

In view of the great latitudinal spread of Baja California and of the wide variety of habitats and oceanographic conditions, it is remarkable that so very few species of fish are confined to the outer coast of the peninsula. Excluding for the moment the fauna of the offshore islands, principally Guadalupe, the west-coast fauna of Baja California includes only a minimal number of forms that have been indicated as restricted endemics. A few littoral clinids are slightly differentiated (Hubbs, 1952, 1953; Springer, 1958); namely, *Paraclinus integripinnis zacae* Hubbs, in west-central Baja California and the offshore islands; *Paraclinus walkeri* Hubbs, from Bahía San Quintín; *Exerpes asper magdalenensis* Hubbs, from Bahía Magdalena; *Exerpes asper earli* Hubbs, from bays in central Baja California; and *Labrisomus wigginsi* Hubbs, from southwestern and west-central Baja California, *Labrisomus xanti* Gill, *Malacoctenus gigas* Springer, and two subspecies in *Malacoctenus* are confined to the same region plus the Golfo de California area. The nominal atherinid species *Leuresthes crameri* Jordan and Evermann appears to be invalid. The one gobiesocid indicated as confined to the mainland west coast of the peninsula, namely *Rimicola dimorpha* Briggs (1955), I have found also on the Channel Islands of California. Three deep-sea bottom fishes have been described only from off western Baja California, namely: (1) *Raja microtrachys* Osburn and Nichols (1916: 142–143, Fig. 1; see also Townsend and Nichols, 1925: 6); (2) *Harriotta curtissjamesi* Townsend and Nichols (1925: 6–8, Fig. 2); and (3) *Coryphaenoides albatrossus* Townsend and Nichols (1925: 17, Pl. 4, Fig. 2), a representative of a group in need of revision in North America. It is extremely improbable that any of these is confined to waters off the peninsula; the distinctness of the chimaeroid from *Harriotta raleighana* Goode and Bean of the Atlantic has been questioned by Bigelow and Schroeder (1953: 551). It seems highly probable that only a few forms of fishes are confined to the outer coast of Baja California, and that these are only slightly differentiated.

Greater local differentiation is exhibited by the fishes of the offshore islands—Guadalupe (oceanic) and the San Benitos (continental). No endemic fishes are known from the islands closer to shore. Some may be found about Rocas Alijos when the fish fauna of these offshore pinnacles (off southern Baja California) is explored. Some of the offshore banks and seamounts may also yield endemics, but their faunas have scarcely been touched (Hubbs, 1959b).

Two well-defined species that seem to be absent along the mainland occur on Guadalupe and the San Benitos, and nowhere else, so far as known. These are a clinid blenny, *Gibbonsia norae* Hubbs (1952), and a relatively deep-water butterflyfish, *Chaetodon falcifer* Hubbs and Rechnitzer (1958) (soon to be reported from Islas San Benito by me).

Several littoral fishes have been described from and appear to be restricted to Isla Guadalupe, which rises out of deep water more than 100 miles off Baja California Norte, and a considerable number of others (see list in Hubbs and Rechnitzer, 1958) exhibit varying degrees of differentiation and will in due time be distinguished. The forms already named as endemic from Guadalupe are:

Raja microtrachys Osburn and Nichols (1916:142–143, Fig. 1), originally ascribed to Guadalupe Island, but shown by Townsend and Nichols (1925: 6) to have come from deep water near Lat. 31° N.

Apogon guadalupensis (Osburn and Nichols, 1916: 160, Fig. 9). This species has been reported also from Cabo San Lucas (Breder, 1936: 18), but material recently collected there seems different.

Atherinops affinis guadalupae Hubbs (1918: 435–437), a well-defined subspecies. The local form of Islas San Benito is quite different, and much closer to *A. a. cedroscensis* of Cedros Island and the open coast thence northward to southern California (except for the two species shared with Isla Guadalupe, this local atherinid is the only fish on the San Benitos that shows evidence of endemicity).

Brachyistius aletes (Tarp, 1952: 89–90), a valid species.

Azurina hirundo Jordan and McGregor (in Jordan and Evermann, 1898: 1544–1545). This species was described as alone representing a district genus, but *Azurina* has since been found on other islands. Critical comparisons are needed to determine endemicity.

Scorpaena guadalupae Fowler (1944: 429–430, Figs. 217–218). This nominally endemic form proves to occur also in Golfo de California and to be merely the southern subspecies of *Scorpaena guttata* Girard.

Rimicola sila Briggs (1955:79–80, Figs. 5, 96). This distinct species and the next I discovered and distinguished, and supplied to Briggs for description in his monograph of the clingfishes.

Gobiesox eugrammus Briggs (1955: 100–101).

Heterostichus rostratus guadalupensis Hubbs (1952: 115–116, Fig. 43), a rather weakly defined subspecies based on lower meristic counts.

Gibbonsia elegans erroli Hubbs (1952: 151–152, Fig. 63), a subspecies verging on specific distinctness from the mainland subspecies.

Gibbonsia elegans rubrior Hubbs (1952: 152, Fig. 64), a deep-water differentiate (several fishes of the depleted fauna on Guadalupe appear to be in the process of bathymetric speciation).

Most of the Guadalupe endemics seem to be the descendents of waifs that reached this oceanic island from either the north or the south, mostly from the north. The higher incidence of endemism of forms of northern origin may have been due to the elimination during Wisconsin time of endemics of southern origin. The varying degree of differentiation may have resulted either from the length of isolation or from the rate of change. The island is notable also for endemism among the marine algae and some endemics have been discovered among the marine invertebrates. The terrestrial plants, gastropods, and birds exhibit a high incidence of endemism, in part autochthonous, in part of a relict nature.

The marine birds of Guadalupe and other islands off western Baja California also exhibit considerable endemism, as is indicated below. They seem, like most of the endemic fishes of Isla Guadalupe, to be of northern origin.

The almost complete lack of endemism among the marine fishes of the outer coast of Baja California, except on the offshore islands, is attributable in large part to an artificial circumstance, namely, the location of the international boundary. If the boundary had been set near Point Conception, only 2° farther north (about one-fifth of the latitude subtended by the peninsula), the west coast of Baja California would have ranked very high as an area of endemism. The warm-temperate San Diegan fish fauna is rich in endemic genera and species, very largely of remote southern origin.

The Elements in the Fish Fauna of Northwestern Baja California

Most members of the San Diegan fauna occur only south of Point Conception, though a few extend northward beyond this point: some, for example *Otophidium scrippsae* Hubbs, for a short distance; others, as strays or occasionally even in mass movements, in warm years, for longer distances, sometimes as far as Puget Sound; still others, for example *Girella nigricans* (Ayres), as waifs wafted north, in young stages, into cool, rich waters where reproduction is inhibited though good growth occurs; a few others, as residual populations in the warmer bays, particularly Morro and Tomales.

Nearly all fishes here listed as San Diegan have been recorded from northwestern Baja California, and probably all occur for varying distances down the Baja California coast. The two San Diegan species not yet reported from western Baja California are *Argentina sialis* Gilbert, which also occurs in Golfo de California, and *Rimicola muscarum* (Meek and Pierson; see Briggs, 1955), which we have recently taken in Baja California. A small proportion occurs or, as noted above is represented by geminate variants, in the cooler parts of Golfo de California (see also the accompanying paper by Boyd W. Walker).

Not included in the preceding and fol-

lowing tallies of the San Diegan species is a rare species, representing a monotypic genus, that is known only from southern California, but is probably tropical or subtropical. This is the peculiar pipefish, *Dermatostethus punctipinnis* Gill, already mentioned.

A tally of the distinctively San Diegan fish fauna indicates 76 genera and 96 species. Of the 96 species, 21 might almost as well be categorized as members of the fauna of Golfo de California and southward that reach northwestern Baja California and southern California, and at least eight approach the Californian category discussed below; on the other hand, several species attributed to each of these other categories might have been included on the San Diegan list. In addition, the San Diegan list includes two subspecies of southern and two of northern relationships. Twenty-two of the genera listed as San Diegan are endemic, in the sense of being essentially confined to southern California and adjacent Baja California, with or without representation in Golfo de California.

Most of the San Diegan fishes are confined in Mexico to Baja California Norte north of the warmish Bahía Sebastián Vizcaíno, but some extend farther, particularly in the areas of moderate upwelling south of Punta Eugenia and on the open coast opposite Bahía Magdalena. The following discussion is based largely on the fauna of northwestern Baja California north of Bahía Sebastián Vizcaíno, for which the data are more complete than for the more southern coast.

A considerable proportion of the fish fauna of the shores and ocean bottoms of northwestern Baja California (north of Bahía Sebastián Vizcaíno) can be classed as a Panamic element, as the forms involved are chiefly characteristic of Golfo de California and more southern waters. A tally of these forms, including a very few known from the Panamic region and California but not yet from anywhere on the outer coast of Baja California, discloses 58 genera and 65 species. As might be expected, from the circumstances that the waters of southern California are warmer than those of northwestern Baja California, except locally, nearly all of these warm-water fishes also occur in southern California, either regularly or sporadically, or did so during the warm period of the nineteenth century. The three definite exceptions encountered are *Achirus mazatlanus* (Steindachner), which is known north of Bahía Sebastián Vizcaíno from a single specimen collected barely south of the international border; *Moebia promelas* (Gilbert), a deep-water brotulid; and *Mugil curema* Valenciennes, the wide-ranging tropical American white mullet, which rarely ranges northward in the prejuvenile querimana stage.

Another large element in the shore and deep-bottom fishes of Baja California north of Bahía Sebastián Vizcaíno are members of what we may call the Californian fauna, in that its members commonly inhabit both the warm-temperate San Diegan and the cool-temperate Montereyan regions (some of the decisions as to placement in this as contrasted with the San Diegan element are somewhat dubious or arbitrary). A tally of this category totals 35 genera (19 endemic) and 62 species. The whole family Embiotocidae is largely characteristic of this fauna. A few species of this list occur also in the cooler parts of Golfo de California, but concerning only one, *Myliobatis californica* Gill, is there any question of a possibly sounder allocation in the subtropical and tropical element. Other species designated Californian range at times as far north as Puget Sound, but are hardly to be included in the Californian-Vancouveran faunal element.

Still other shore and deep-bottom fishes of northwestern Baja California can be allocated in what may be termed Californian-Vancouveran and Californian-Alaskan elements. A tally of these categories totals 50 genera (27 endemic) and 60 species, of which eight are rare enough,

as immigrants or wanderers from the south, to be perhaps more reasonably classed as Californian. One of the species included, the deep-water alepocephalid *Narcetes stomias* (Gilbert), was described from off Washington, and has since been definitely recorded only from off northern Baja California (by Townsend and Nichols, 1925: 10, who question its possible identity with a Panamanian species).

Still more northern in affinity, among the fishes of northwestern Baja California, are the following Pacific amphiboreal fishes:

Squalus suckleyi (Girard), the Pacific spiny dogfish, by some now synonymized with *S. acanthias* Linnaeus of the North Atlantic.

Oncorhynchus kisutch (Walbaum), silver salmon, a rare stray below the California border.

Cololabis saira (Brevoort), the Pacific saury, essentially pelagic (genus endemic).

Coryphaenoides acrolepis (Bean), a deep-water macrourid, of a species group requiring revision.

Icichthys lockingtoni Jordan and Gilbert, the medusafish (genus endemic).

Icosteus aenigmaticus Lockington, the ragfish (genus endemic).

Pneumatophorus japonicus (Houttuyn), the Pacific mackerel, as a species.

Zesticelus profundorum (Gilbert), a deep-sea sculpin (genus endemic).

A summary by faunal elements of the genera, endemic genera, and species of the inshore and deep-bottom fishes of Baja California north of Bahía Sebastián Vizcaíno (Table I) indicates the essentially northern character of the fauna, particularly in respect to endemic genera (most of the species are endemic to each specified element). The high endemicity of the genera in the northern elements reflects the enormous richness and high distinctiveness of the North Pacific temperate-to-boreal fauna. The lack of endemic genera in the Panamic element that is represented in the fauna of northwestern Baja California reflects not only the low degree of generic endemism in that element but also its relative impoverishment, except in a few families, most notably in certain groups inhabiting inshore

TABLE I—TALLY OF GENERA, ENDEMIC GENERA, AND SPECIES IN EACH OF THE ELEMENTS IN THE INSHORE AND DEEP-BOTTOM FISH FAUNA OF NORTHWESTERN BAJA CALIFORNIA.

ELEMENT	GENERA	GENERA ENDEMIC TO STATED ELEMENT	SPECIES
Panamic	58	0	65
San Diegan	76	21	96
Californian	35	19	62
Californian-Vancouveran Californian-Alaskan	50	29	60
Pacific Amphiboreal	8	4	8

sandy and muddy waters, such as Engraulididae, Ariidae, and Sciaenidae. Very few of the tropical species of these families range north of the southern margin of Bahía Sebastián Vizcaíno. The low generic endemism in the Panamic fauna is due in considerable part to the circumstance that the Panamic fauna is largely a part of the common Atlantic-Pacific tropical fauna of the New World, with a few Indo-Pacific intrusions.

The notable admixture of tropical and subtropical as well as San Diegan, Montereyan, Californian, and Vancouveran fishes in the fauna of western Baja California is attributable to the striking local differences in present surface temperatures, to the marked seasonal and annual fluctuations, and to extensive latitudinal shifts during Pleistocene and Holocene times.

The Marine Reptile Fauna

I have no certain record of the sea snake *Pelamis platurus* (Linnaeus) from the west coast of Baja California, but it probably occurs along that coast for some distance north of the Cape. At times it is extraordinarily common as far north as Puerto Vallarta on the mainland coast of Mexico.

All sea turtles of the eastern Pacific probably occur at least occasionally along

the west coast of the peninsula. The eastern Pacific green turtle, *Chelonia mydas agassizii* Bocourt, supports a fishery as far northward as Bahía Sebastián Vizcaíno, is said to have occurred in Bahía San Quintín, and wanders occasionally, in warm years in some numbers, as far as southern California. The Pacific hawksbill turtle, *Eretmochelys imbricata squamata* Agassiz, occurs about La Paz and no doubt at times wanders into southwestern Baja California. The Pacific loggerhead turtle, *Caretta caretta gigas* Deraniyagala, occasionally reaches southern California, though much less frequently than the green turtle. The Pacific ridley, *Lepidochelys olivacea* (Eschscholtz), has not been recorded from the west side of the peninsula, but must have transgressed that side, for during the recent warm period one appeared in northern California (Houck and Joseph, 1958). The Pacific leatherback turtle, *Dermochelys coriacea schlegelii* (Garman), has been taken along the northwestern coast of Baja California, and occasionally wanders much farther, even to British Columbia (Carr, 1952).

The Marine Bird Fauna

As already indicated nearly all marine birds that breed or migrate as far south as the San Diego region at least occasionally occur along the cooler coast of northwestern Baja California. Similarly, most of the sea birds of southern affinity that occur along that area of upwelling transgress the international border. A number of species that occur northward only to southern or (a few) to central Baja California, appear to be wholly or largely blocked in their northward dispersal by the conditions that are associated with this upwelling. Most of the species that are limited in northward dispersal are definitely tropical, and add to the tropical stamp of southwestern Baja California.

The distributional relations involved are briefly presented in the following statements, derived largely from the data of Grinnell (1928), Friedman, Griscom, and Moore (1950), and Blake (1953).

The least grebe, *Colymbus dominicus bangsi* van Rossem and Hachisuka, a species of brackish and fresh waters, has been reported from the Cabo San Lucas region but not farther north on the outer coast.

The Pacific shearwater, *Puffinus pacificus chlororhynchus* Lesson, is a tropical species recorded in the Cape region but not farther north on the outer coast.

The Revillagigedo shearwater, *Puffinus auricularis* Townsend, is recorded with some doubt north to the Cape region.

The blue-footed petrel, *Pterodroma cookii orientalis* Murphy, has been reported northward only to off Cabo San Lucas.

The storm petrel, *Oceanodroma tethys tethys* (Bonaparte), wanders north to off Baja California, and has once been found breeding on Guadalupe Island (Huey, 1952).

The red-billed tropicbird, *Phaethon aethereus mesonauta* Peters, is fairly common north to the Cape region, but rare north to California.

The red-tailed tropicbird, *P. rubricauda rothschildi* (Mathews), is rare off northwestern Baja California, but is unknown from California.

Two of the three boobies, *Sula dactylatra californica* Rothschild and *S. leucogaster brewsteri* Goss, that occur occasionally along the western coast of Baja California have not been found north along the coast as far as California, unless, as seems likely to me, the old reports discredited by Grinnell and Miller (1944: 558) represent authentic records at a time when the southern fauna was dispersed far northward (Hubbs, 1948).

The magnificent frigatebird, *Fregata magnificens rothschildi* Mathews, and the thick-billed plover, *Charadrius wilsonius beldingi* Ridgway, are common along the southwestern coast of Baja California, but are rare farther north (as far as California).

The sooty tern, *Sterna fuscata crissalis* (Lawrence), is another tropical species that is known northward only to off southwestern Baja California.

The elegant tern, *Thalasseus comatus* (Philippi and Landbeck), is resident north to west-central Baja California, and is a post-breeding visitant into California.

Considerable insular endemism characterizes the marine avifauna of Baja California.

The now extinct Guadalupe petrel, *Oceanodroma macrodactyla* Bryant, apparently bred

only on the forested mountain top of Isla Guadalupe.

The Baja California breeding populations of the Leach petrel, *Oceanodroma leucorhoa* (Vieillot), all confined to islands, have distinctive characters. *Oceanodroma l. willetti* van Rossem of Islas Los Coronados and *O. l. chapmani* Berlepsch of Islas San Benito may comprise a single form not known to breed elsewhere. On Guadalupe Island there are two separable forms, of similar size, smaller than any of the other subspecies. One, probably to be identified with *O. l. socorroensis* Townsend, which has the rump largely dark, and thus approaches the subspecies of the Coronados and the San Benitos, breeds in the summer. The other Guadalupe subspecies, *O. l. kaedingi* Anthony, breeds in the same places, even in the same burrows, but disjunctively in the winter. The segregation is temporal, not spatial.

The Heermann gull, *Larus heermanni* Cassin, is confined during breeding to only one island, San Roque, along the west coast of Baja California, and to several islands in Golfo de California.

The resident western gulls, *Larus occidentalis* Audubon, of Guadalupe Island contrast with the migrants from the north, *L. o. wymani* Dickey and van Rossem, in having feet very pale (whitish, yellowish, or barely pink), rather than distinctly pink, but not definitely yellow as in the Gulf form, *L. o. livens* Dwight. However, since western gulls from the central and southern parts of the west coast of Baja California are also in part light-footed, the problem is not yet settled.

The three forms of the alcid genus *Endomychura,* commonly assigned subspecific rank but perhaps better regarded as full species, are all insular endemics, largely of Baja California. *Endomychura hypoleuca hypoleuca* (Xantus) apparently breeds only on Isla Guadalupe; *E. h. scrippsi* Green and Arnold reproduces on several islands nearer to the mainland, from the Channel Islands of California to Islas San Benito off central Baja California; *E. craverii* (Salvadori) breeds only on islands in Golfo de California.

Another insular endemic alcid has been described from Baja California. This is *Ptychoramphus aleuticus australis* van Rossem, which breeds on islas San Benito and San Roque. The typical subspecies of the Cassin auklet breeds as far south as islas San Gerónimo and Guadalupe.

The Marine Mammal Fauna

The marine mammals furnish some of the most interesting and significant data bearing on the zoogeography of the outer coast of Baja California.

Five northern species reach their southern limit of distribution in the cool waters off northwestern Baja California. These include: (1) the southern sea otter, *Enhydra lutris nereis* (Merriam), which formerly ranged to Isla Cedros (but is now extinct south of San Miguel Island, California); (2) the northern fur seal, *Callorhinus ursinus* (Linnaeus), which migrates as far south as between islas Guadalupe and San Benito (personal observation); (3) the California harbor seal, *Phoca vitulina geronimensis* Allen, which occurs on the rocky reefs and in bays north of Bahía Sebastián Vizcaíno; (4) the striped porpoise, *Lagenorhynchus obliquidens* Gill; and (5) the Dall porpoise, *Phocoenoides dalli* True, both of which range well into the cool waters of northwestern Baja California, but no farther.

Three pinnipeds find their center of abundance off the northern half of the west coast of Baja California, but range, or primitively did range, beyond the limits of Baja California, both north and south. These are: (1) the California sea-lion, *Zalophus californianus* Lesson, which still ranges far north of Baja California, has a very small disjunct remnant population in the Sea of Japan (probably dating from Interglacial dispersal), originally ranged south of its present limit in the regions of Cabo San Lucas and Islas Tres Marías, and is represented in the Galápagos by a subspecies, *Z. c. wollebaeki* Sivertsen; (2) the Guadalupe fur seal, *Arctocephalus townsendi* Merriam, which seems always to have had its center of abundance on Isla Guadalupe, to which it now is restricted; and (3) the northern elephant seal, *Mirounga angustirostris* (Gill), which has rebuilt its population on Guadalupe to about 13,000 and is reestablishing colonies on other islands off northern Baja California and southern California, wanders north to southeastern Alaska, and is reported to have occurred

on Clipperton Island. The Pacific bottlenose porpoise, *Tursiops gillii* Dall, seems also to have its center of abundance along the west coast of Baja California.

Of outstanding interest is the almost complete restriction of the east Pacific population of the gray whale, *Eschrichtius gibbosus* (Erxleben), during the calving season, to the lagoons along the west coast of Baja California. This unique species is here a relict, for the species existed prehistorically in northern Europe and in early historic time in the western North Atlantic, and still persists in limited numbers in the northwestern Pacific. Very limited breeding populations occur on the mainland coast of Mexico near the mouth of Golfo de California, and occasionally calves are born about Isla Guadalupe and along the coast of southern California, though San Diego Bay has been abandoned as a breeding locale.

Most of the wide-spread cetaceans of the North Pacific—ziphiids, delphinids, physeterids, and balaenopterids—either are known to occur off western Baja California or may be expected there. A recent addition to the list is the grampus, *Grampidelphis griseus* (Cuvier), which we recently observed in company with sperm whales at Isla Guadalupe.

Summary

As a first, crude approximation the Gulf coast and Cape region of Baja California may be included in the Panamic Province and the rest of the outer coast in the warm-temperate San Diegan division of the Californian Province. The transition is neither abrupt nor regular. The Cape region has a reduced tropical fauna, with some Indo-Pacific types, and insular characteristics. In conformity with oceanographic conditions, the tropical elements of the fauna persist much farther northward in the Gulf than on the outer coast, where they decline abruptly between the Cape and Bahía Magdalena. Northward, tropical elements tend to persist in bays, whereas northern types extend southward along the open coast, where temperatures are lowered by upwelling; any definite faunal boundary lines would violate some facts of distribution. Many tropical forms reach the southern shore of Bahía Sebastián Vizcaíno, a few extend farther, especially in warm years (as 1957–1959). Northward dispersal and warm temperatures were especially pronounced about a century ago. Warm-temperate (San Diegan) types persist in upwelling areas to near Bahía Magdalena (a few at the Cape); cool-temperate (Montereyan) types occur, some after skipping southern California, in the very cool open shores of northwestern Baja California. Differences are notable between the temperatures and the biota on the two sides of headlands.

The general pattern of distribution, though conservative, has been much modified by latitudinal shifts, most notably during the Pleistocene. During Glacial periods the fauna was displaced southward, to yield Pleistocene relicts in the upper Gulf. Interglacially, there were northward dispersals, indicated, for example, by a warm-water Pleistocene fauna on Guadalupe Island.

Endemism is remarkably slight among the fishes of the outer coast of Baja California, but would have been high if the international border had been fixed 2° of latitude farther north, near Point Conception (roughly the northern limit of the very distinctive San Diegan fauna). Endemism is noteworthy among the marine vertebrates of Isla Guadalupe, which is oceanic and more than 100 miles offshore.

The fauna of the northwestern coast of Baja California, which is cooled by upwelling, contains a limited number of Panamic types, almost none of which are Panamic endemics, and almost all of which occur at least occasionally in the waters of southern California, which are warmer. There is a much larger representation of northern elements, San

Diegan, Californian, Californian-Vancouveran, and Californian-Alaskan, with a few Pacific amphiboreal forms. In each of these elements, a considerable proportion of the genera are endemic to the given element. These circumstances reflect the immense richness and distinctness of the North Pacific fauna.

The notable admixture of tropical and subtropical as well as San Diegan, Montereyan, Californian, and Vancouveran fishes in the fauna of western Baja California is attributable to the striking local differences in surface temperatures, the marked seasonal and annual fluctuations, and the extensive latitudinal shifts during Pleistocene and Holocene times.

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Symposium: The Biogeography of Baja California and Adjacent Seas

PART III. TERRESTRIAL AND FRESH-WATER BIOTAS

The Origin and Relationships of the Land Flora

IRA L. WIGGINS

VERTICAL oscillations of the peninsula of Baja California between Cretaceous and Pleistocene time have resulted in alternate flooding and emergence of about one-half of its area, and have profoundly influenced the composition of its present flora. Obviously, the vegetative cover in a region flooded by invading seas during the Miocene period had to be reestablished after the last recession of salt water, and must have drawn its flora largely from adjacent areas not drowned out while the peninsula was partially submerged.

Judging from the maps presented by Durham and Allison, the inundations and emergences of the peninsula since the Eocene period left four main regions above the highest lines of flooding to form refugia where land plants and animals have been able to live continuously throughout the Tertiary. In descending order of size, these regions are (a) the mainland of Mexico; (b) a large proportion of the northern half of the peninsula; (c) the mountains of the Cape region of Baja California; and (d) the western part of the Vizcaíno Desert and the immediately adjacent islands northwest of that region.

Essentially, only the southern tip of the peninsula has been isolated from the main reservoir of plant material on the mainland of Mexico and in the California-Rocky Mountain regions to any marked degree. Between the Cape region and the Sierra San Pedro Mártir, the peninsula consists of low but rugged mountains paralleling, and in close proximity to, its eastern shores, and of gently sloping plains lying inland from the Pacific Coast. This is a region where the floristic elements from the north, and those persisting in the Cape refugium during the Miocene inundation, have intermingled and competed from early Pliocene time to the present. Incomplete information about the flora in the Sierra de San Francisquito and in the Sierra de la Giganta hampers attempts to trace lines of migration, but there exists evidence that there were northward, as well as southerly, migrations along this mountain chain. For example, the genus *Alvordia,* endemic in Baja California (Fig. 9), has the center of its distribution in the Cape region, but

one species extends northward to the vicinity of Santa Rosalia.

Paleobotanical information from the peninsula is scanty, so assumptions and deductions regarding the modern flora of Baja California must, at present, be based primarily on phytogeographic studies of modern species, and on the relationships existing between them and the same, or closely related species, living in other parts of the continent or of the world. Without doubt, much information obtained through paleobotanical studies of fossil floras from the southwestern parts of the United States and comparison of such fossil floras with modern floras from areas farther to the south is applicable to portions of Baja California, and may hold keys to some of the phytogeographic problems associated with investigations of its flora. However, interpretations of the floristic relationships of the peninsula could be made with greater assurance if a few fossil floras were to be found in Baja California and compared with ones already known from other southwestern localities. The investigations of Chaney (1938, 1947), Mason (1947), Axelrod (1938, 1950a, 1950b, 1958, 1959), and others, hold intriguing possibilities for untangling some of the phytogeographic puzzles in the peninsula. More extensive —and intensive—field work in Baja California may reveal paleobotanical deposits that can shed much light on problems still unsolved.

Phytogeographic Areas in Baja California

There are three relatively distinct modern floral complexes in Baja California: (1) the Californian, occupying the foothills and mountains west of the San Felipe Desert and extending southward from the International Boundary to the southern tips of the Sierra de San Pedro Mártir; (2) The Cape region flora (Shreve, 1937), occupying chiefly the area south of La Paz, but sending some aggressive migrants northward through the Sierra de la Giganta; and (3) the Central Desert flora occupying the area lying between the first two and sending a narrow band north through the San Felipe Desert into southern California and Arizona, and with a small "island" along the easternmost margin of the Cape region south of La Paz (Fig. 1). Axelrod (1950a, 1958) has postulated derivation of all of these floras from the Madro-Tertiary geoflora of central Mexico.

In many respects the most intriguing of these floristic assemblages is the third, the Desert flora. It contains a number of endemics, has produced some fascinating adaptations to arid conditions, and lives where the conditions for growth, reproduction, and existence are nearly always marginal. This desert flora can be subdivided further into four reasonably well marked subfloras (Fig. 2): (a) the San Felipe Subflora; (b) the Central Gulf Coast Subflora; (c) the Vizcaíno Desert Subflora; and (d) the Magdalena Plains Subflora. These subfloras deserve a brief outline of the characteristics of each.

(a) *The San Felipe Subflora* occupies what Shreve (1951) called the *"Larrea-Franseria* Region," that part of the lower valley of the Colorado River east of the Sierra de Juarrez and the Sierra de San Pedro Mártir. This region has the lowest average rainfall and the highest percentage of sunshine per day and month of any of the peninsular subregions. It occurs in an area of diversified physical features, with soil derived from volcanics, granitic rocks, and from alluvial deltaic deposits. It includes sandy plains and extensive areas covered with sand dunes; alkali flats; barren volcanic craters; broad outwash "bajadas" at the mouths of the canyons leading down from the mountains to the west; and esteros with their banks deeply encrusted with salt. In this area the desert spacing of the shrubs and perennial herbs is marked, with scarcely any perennial plant touching the territory occupied by its nearest neighbor. *Larrea tridentata* and *Franseria dumosa* are outstandingly the dominant species, with as

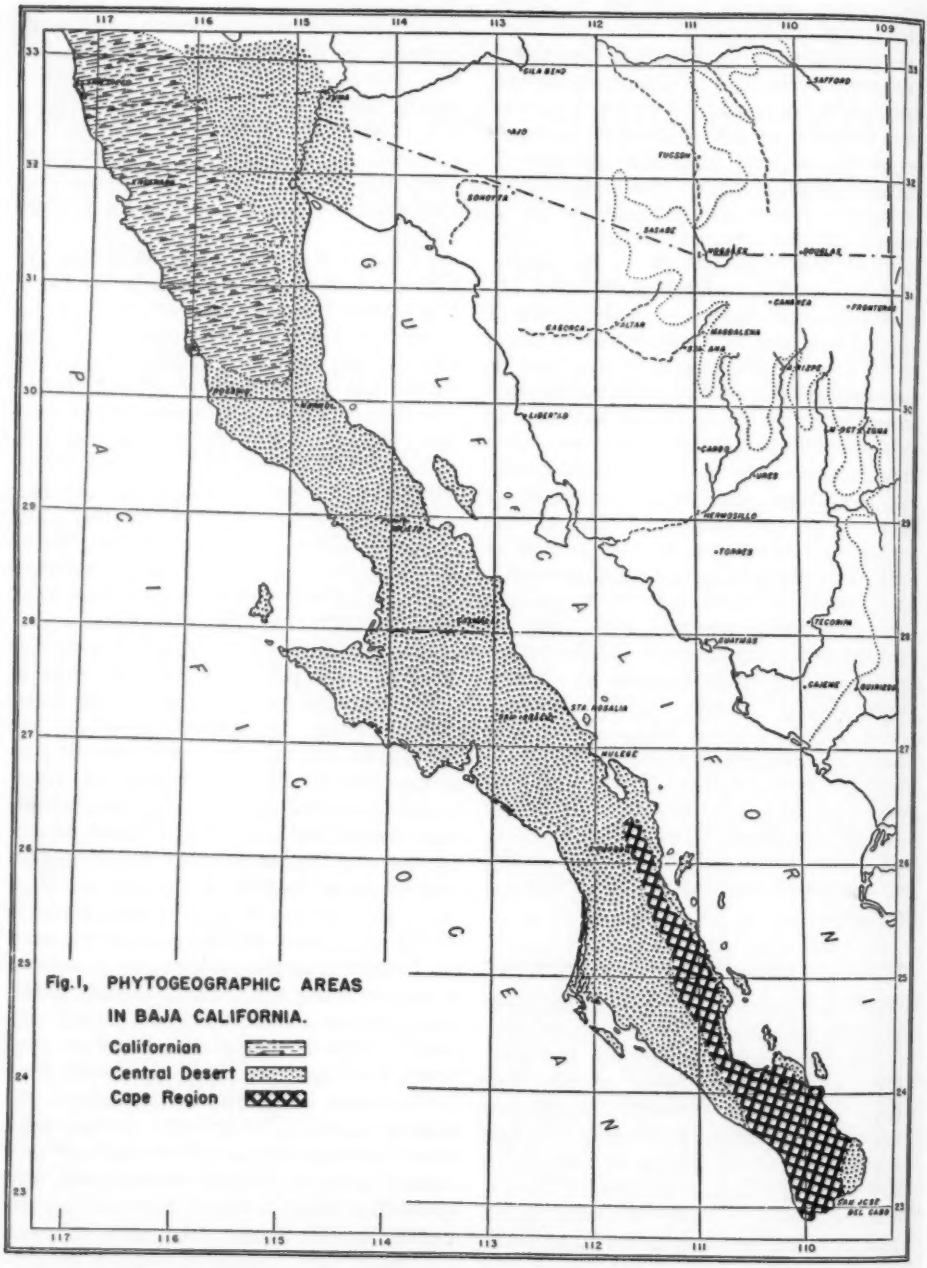
Fig. I, PHYTOGEOGRAPHIC AREAS
IN BAJA CALIFORNIA.
Californian
Central Desert
Cape Region
PACIFIC OCEAN
GULF OF CALIFORNIA

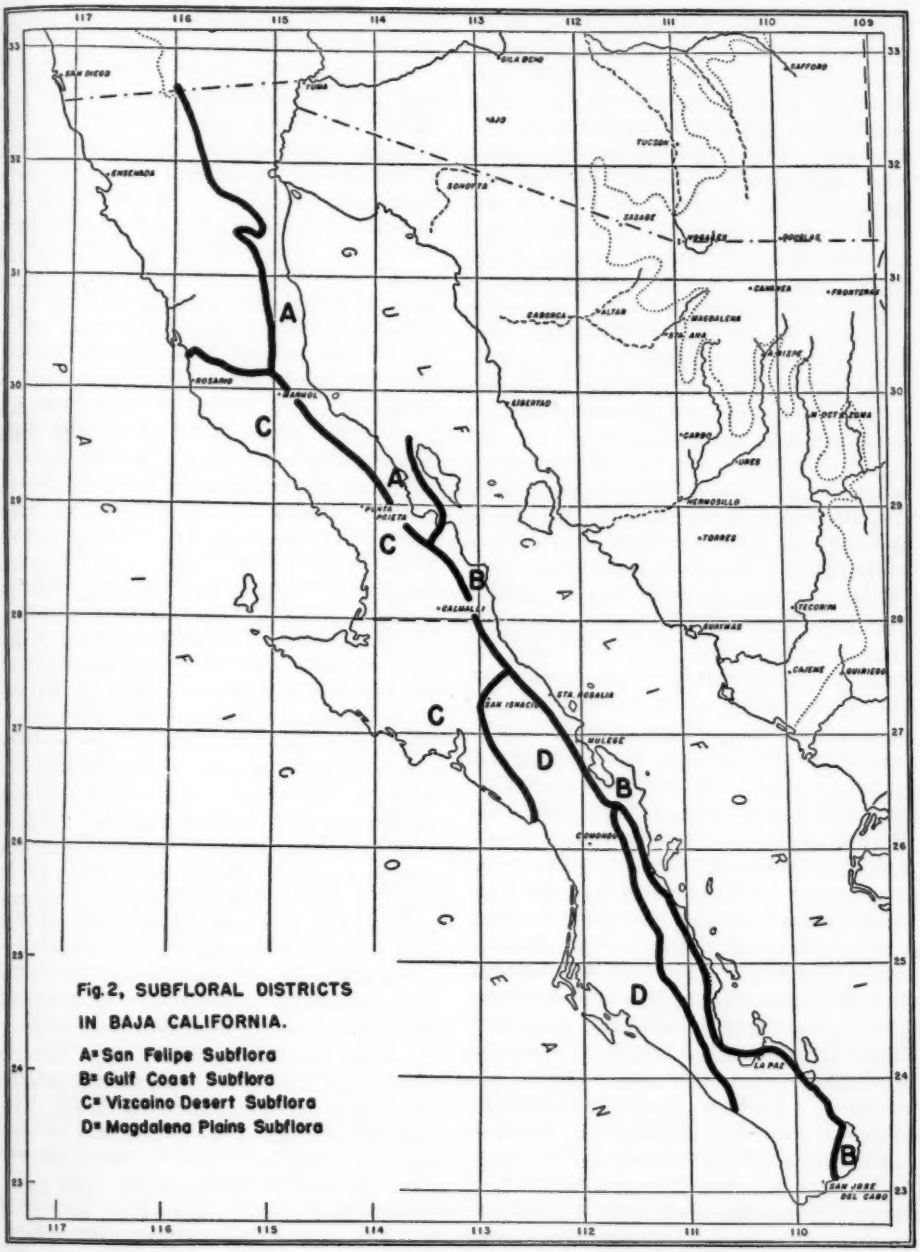
A
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Fig. 2, SUBFLORAL DISTRICTS
IN BAJA CALIFORNIA.
A= San Felipe Subflora
B= Gulf Coast Subflora
C= Vizcaino Desert Subflora
D= Magdalena Plains Subflora

much as 90% of the total ground cover made up of their representatives. Other plants of importance and contributing to the phytophysiognomy of the region are *Prosopis juliflora* var. *torreyana, Cercidium microphyllum, Olneya tesota,* several cacti, and following the infrequent rains—sometimes several years apart—large numbers of annual herbs that provide a brief display of color. Botanical exploration of this area has been scanty in the past, but a newly constructed road connecting San Felipe with the main north-south road running down the western side and center of the northern peninsula, will permit more thorough investigation of its southerly expanses than have been practical up to this time. Air reconnaissance between San Felipe and El Marmol has indicated that there may be intensely interesting material in some of the canyons and along arroyos in and adjacent to this poorly explored area.

(b) *The Central Gulf Coast Subflora* occurs in an area of relatively to markedly rugged terrain, where volcanic and granitic ground rock intermingle intricately, and where rains are unpredictable and may occur during either summer or winter (Fig. 2). Hence, the response of plants to rainfall is sporadic rather than seasonal, and whereas January may offer the best collecting one year, favorable conditions may occur in August or November during another. The vegetation has been characterized as that of the *"Bursera-Jatropha* Region" (Shreve, 1951), for *Bursera microphylla, Bursera hindsianum,* and *Jatropha cinerea* are the dominant plants over much of its extent, and *Idria columnaris, Olneya tesota, Fouquieria splendens, F. peninsularis, Larrea tridentata, Viscainoa geniculata, Encelia farinosa, Franseria magdalenae, Euphorbia misera, Pedilanthus macrocarpus, Opuntia cholla, Pachycereus pringlei,* and *Opuntia clavellina* contribute importantly to the general vegetational cover over considerable areas—or in specialized limited habitats. Close relationships exist between this subflora and the flora of the Sonoran-Chihuahuan Desert areas across the Gulf of California (Shreve, 1942).

(c) *The Vizcaíno Desert Subflora* makes up the vegetative cover of Shreve's (1951) *"Agave-Franseria* Region." Although bordered by the Pacific Ocean along its westerly shore, it is only slightly influenced by maritime factors. The distance to the mountains along its eastern border, and the gradual ascent from sea level to the relatively low mountain crests from west to east, account for the comparatively insignificant maritime influence. The coastal vegetation is scanty, widely spaced, and much of it shows unmistakably the effects of strong, almost continuous winds that release very little moisture in their passage. Several species of *Agave, Franseria chenopodifolia, Yucca valida, Opuntia cholla,* and two or three species of *Dudleya* are the dominant plants over much of this area. *Idria columnaris, Pachycormus discolor, Pachycereus pringlei, Viscainoa geniculata, Echinocereus brandegeei, Viguera deltoidea, Machaerocereus gummosus,* and *Franseria magdalenae* occupy important niches in the appropriate habitats. Heavy burdens of epiphytic *Tillandsia recurvata* resemble birds' nests of ancient vintage on many of the shrubs near the coast, and others are well covered with the dye-producing lichen, *Rocella.* These epiphytes nearly smother the shrubs in some areas and the *Rocella* was an important source of dye prior to the development of the aniline industry (Nelson, 1921).

Triteleiopsis palmeri is an attractive and seasonally conspicuous endemic of the area following periods of good rainfall. Its large umbels of bright blue flowers would add beauty to gardens where light sandy soil and good drainage occur. The graceful, slender-trunked fan palm, *Washingtonia robusta,* occurs in the northerly parts of this district, and the blue palm, *Glaucothea armata,* grows in scores of canyons on both the westerly and easterly slopes of the mountains along its eastern border.

The derivation of the species making up this subflora is mixed, with some genera having their closest relatives in the Californian region, many having close ties with genera in the Sonoran-Chihuahuan Desert areas, and some apparently derived from the subtropics of Mexico and Central America. Endemic species within the region supporting this subflora are numerous and in some instances relationships are difficult to establish with confidence.

(d) *The Magdalena Plains Subflora* occupies the area Shreve (1951) called the *"Lysiloma-Machaerocereus* Region." *Machaerocereus gummosus* is dominant throughout the area, *M. eruca* is plentiful in sandy areas along parts of the western portions of the plains, but *Lysiloma* occurs as a dominant chiefly along canyons in the Sierra de la Giganta but occasionally follows the arroyos some distance into less rugged terrain. Cacti are prominent, with *Pachycereus pringlei, Lemaiereocereus thruberi, Opuntia comonduensis, O. cholla, Pereskiopsis porteri,* and *Mammillaria peninsularis* giving character to the vegetative mantle. Non-succulents of importance include *Bursera laxiflora, Cercidium peninsulare, Jatropha cinerea, Lycium brevipes, Pithcellobium confine, Esenbeckia hartmannii,* and *Fouquieria peninsularis. Burragea* is endemic on the Magdalena and Santa Margarita Islands, and both *Tillandsia* and *Rocella* are common on many of the shrubs.

There are strong relationships between the flora of the Magdalena Plains and that of central and southern Mexico, and some with the Sonoran-Chihuahuan Desert areas.

These four subfloras of the desert areas intergrade gradually from one into the next, so there is no sharp line of demarcation between them. *Larrea tridentata, Cercidium microphyllum, Encelia farinosa, Jatropha cinerea, Asclepias subulata,* and various species of *Opuntia* are common to all, but the combinations of other species vary from one region to another. Several endemic genera and many endemic species occur within these desert subfloras, although the percentage of the total flora made up of endemics is probably slightly lower than it is in the Cape region.

Two of the areas occupied by these subfloras are imperfectly known botanically, namely, the western portions of the Vizcaíno desert and the southern part of the San Felipe desert. More extensive field operations in these regions are needed to reveal the relationships between the plants and the microhabitats of the area and the floristic relationships with the plants of contiguous and more distant parts of the peninsula and Mexico. Such increased exploration may bring to light an indeterminable number of species as yet unknown to science. A program of intensive field work, supported by the Belvedere Scientific Fund in cooperation with the California Academy of Sciences and with other institutions, is now under way and will, it is hoped, provide much additional information of importance about the flora and fauna of the peninsula during the next few years.

Regions of Origin

When one examines the floristic characteristics of the peninsula he finds that there are seven major phytogeographic areas from which elements in the present day flora of Baja California have been derived. Each of the following maps shows the distribution of a genus selected to show the relative concentration of its Mexican and/or American species within and outside the peninsula. The solid lines show the general distribution of species that occur in the peninsula, the dashes that of species of the same genus whose ranges do not reach the boundaries of Baja California.

Californian Phytogeographic Area. The area having the highest representation in the flora of the northernmost part of Baja California is the Californian, from which come such genera as *Adenostoma, Arctostaphylos, Calochortus, Ceanothus, Eriodictyon* (Fig. 3), *Heteromeles, Gilia, Di-*

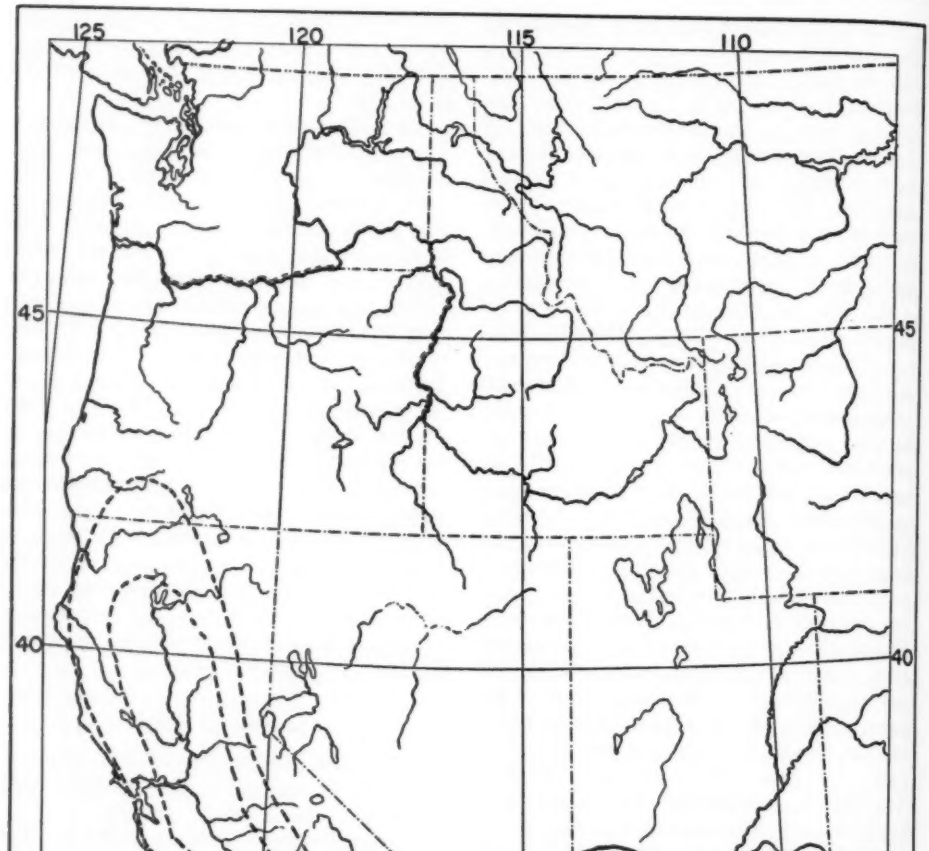

Fig. 3, DISTRIBUTION OF ERIODICTYON

placus, Phlox, Rhamnus, Quercus, Lathyrus, Eriogonum, Umbellularia, Cupressus, and *Populus,* to name only a few. This flora of the northern foothills and mountains is the one that Shreve (1936) called "a transition from chaparral to desert" and which covers most of the area between the San Felipe desert and the Pacific Ocean. It is chiefly a chaparral flora, but there is a montane element in the higher Sierra de Juarrez and in the Sierra de San Pedro Mártir. In it occur such species as *Pinus jeffreyi, P. lambertiana, P. contorta* var. *latifolia, Cupressus montana, Libocedrus decurrens, Populus tremuloides, Woodwardia fimbriata, Cercocarpus betuloides,* and a number of others. As pointed out by Shreve, the influence of the Californian flora wanes toward the southern end of the Sierra San Pedro Mártir and the adjacent foothills, giving way almost entirely to desert elements at about the latitude of Rosario.

The chaparral complex of northern Baja California contains a few endemics that are confined to this area and do not cross into Arizona or northern Sonora. Among them are *Arctostaphylos oppositifolia, Eriogonum vollmeri, Rosa minutiflora, Aesculus parryi, Penstemon palmeri, Atriplex julacea, Opuntia stellata,* and *O. santa mariae.* All of these except the last two clearly are closely related to species occurring north of the International Boundary in California or regions slightly to the east of that area.

Great Basin and Rocky Mountain Phytogeographic Area. This region to the east and north of the chaparral complex in southern California contributes elements to both the chaparral and the montane floristic assemblages. It gives the peninsula *Atriplex tridentata, A. canescens, Eurotia lanata, Juniperus californica, Ephedra nevadensis,* and may be the source of *Populus tremuloides* and *Pinus quadrifolia.* Several grasses also probably migrated into the peninsula from the Great Basin-Rocky Mountain area, among them *Triodia pulchella, Bouteloua* spp., *Sporobolus microsperma,* and species of *Poa, Elymus, Stipa,* and possibly *Cenchrus.* Forbs growing in Baja California that have their main relationships with species in the Great Basin-Rocky Mountain area include *Astragalus, Cryptantha, Chaenactis* (Fig. 4), *Oenothera,* and various members of the Umbelliferae and Compositae. Two factors tend to reduce the importance of this center as compared with that of southern California—the greater migrational distances involved, and the fact that the plants of the Great Basin-Rocky Mountain center are acclimated to low winter temperatures and to some summer rainfall, conditions poorly provided by most of the peninsula.

The Sonoran and Chihuahuan Desert Phytogeographic Area. For our purposes these two desert areas may be considered as a single floristic area, for they are separated by a comparatively narrow band of arid grassland and contain many species common to both. Prior to the Miocene period the Gulf of California is believed to have extended north only about to the latitude of Tiburon Island. Thus direct interchange from the Sonoran area to Baja California was possible until the beginning of the Miocene. Ever since that period the width of the Gulf of California has not been excessive, and at least a few plants must have crossed this barrier. Migration around the head of the Gulf, no doubt, is possible, but the aridity of the lower Colorado River valley has slowed most such migrations and halted others.

Among the plants now occurring in the peninsula and which probably came from the Sonoran-Chihuahuan region are species of *Celtis, Ephedra* (Fig. 5), *Aristolochia, Acacia, Calliandra, Parthenium, Haplopappus, Nolina, Boerhaavia, Maximowiczia,* and *Erythaea.*

Assuming that the chief centers of their distribution indicate places of origin, the more westerly part of this area, namely the Sonoran desert region, may have contributed a number of representatives of such genera as *Acalypha, Randia, Abu-*

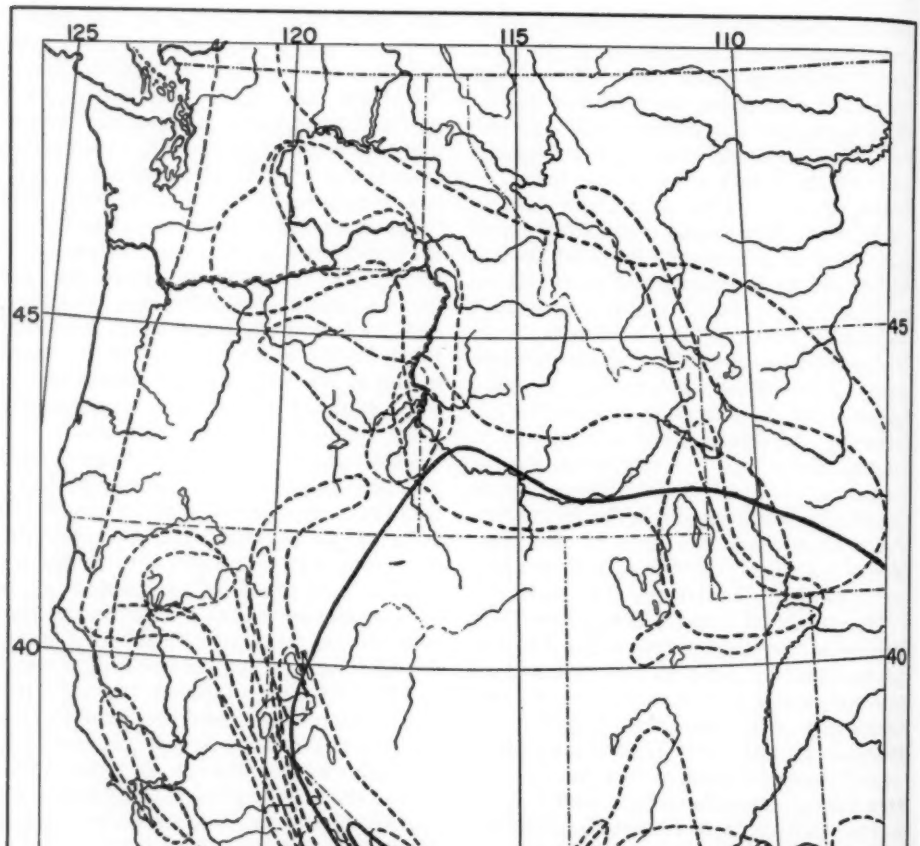

Fig. 4, DISTRIBUTION OF CHAENACTIS

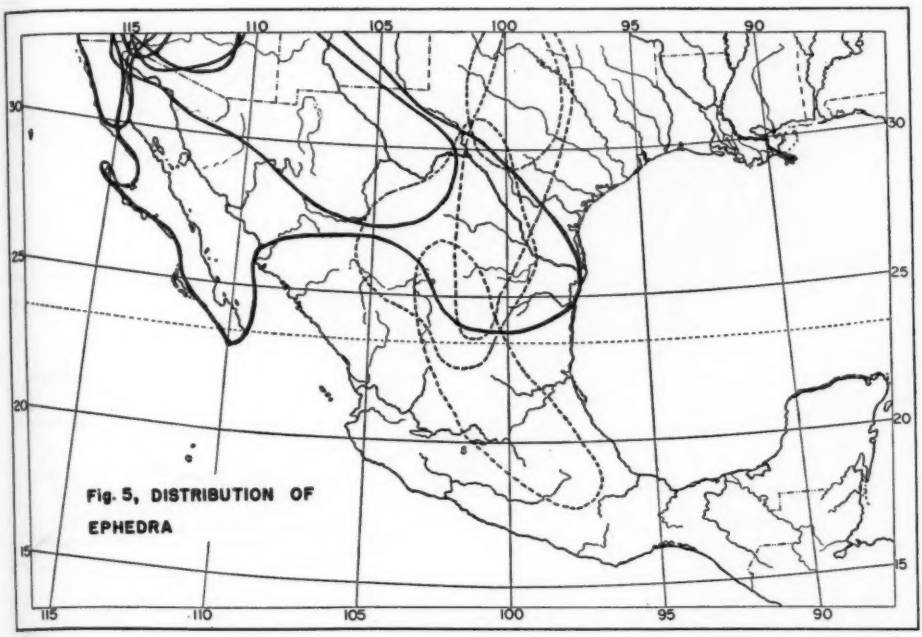

Fig. 5, DISTRIBUTION OF EPHEDRA

tilon, Ipomoea, Lysoloma, Cordia, Ruellia, several cylindrical Opuntias, and *Atamisquea* to Baja California.

The Sierra Madre Phytogeographic Area. This central Mexican plateau is an important reservoir from which plants belonging to a number of families have spread northward and westward to enter the peninsula, and many genera are represented in both areas by the same or closely related species. Among such genera are *Acacia* (Fig. 6), *Calliandra, Fouquieria, Pithecellobium* (Fig. 7), *Mimosa, Karwinskia, Bursera, Bumelia, Maba,* and a number of others. Many of the genera living in the Sierra Madre area today are found widely distributed in other parts of the world as well; witness the presence of *Acacia* in Australia and Africa (from whence they may have come to Mexico), *Solanum* in South America, *Jatropha* and *Euphorbia* from South America and Africa, and a number of members of the Rubiaceae having worldwide distribution.

When there are representatives of such wide-ranging genera present in a flora it is difficult to determine whether a certain element came from a particular district or from an entirely different one. However, it seems clear that the oaks native in the Cape region of Baja California, and the single species of *Arbutus* (Fig. 8) growing there, are more closely related to members of those genera now living in the central Mexican area than they are to representatives of the same genera native to Alta California.

The Southern Mexican Lowlands. This region, which floristically is an extension of the Caribbean area, contributes only a few elements to the flora of Baja California, and most of these occur only in the southern part of the peninsula. Among this small group of species are representatives of such genera as *Bignonia, Cyrtocarpa, Coursettia, Panicum,* a bamboo-like grass or two, etc. The low rainfall throughout most of Baja California, as compared to the more abundant precipita-

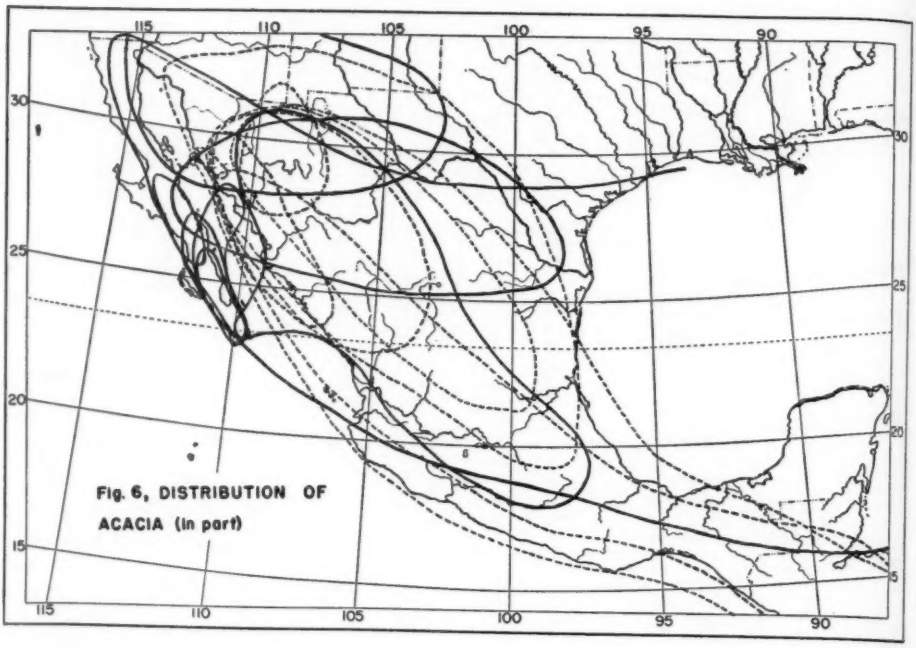

Fig. 6, DISTRIBUTION OF ACACIA (in part)

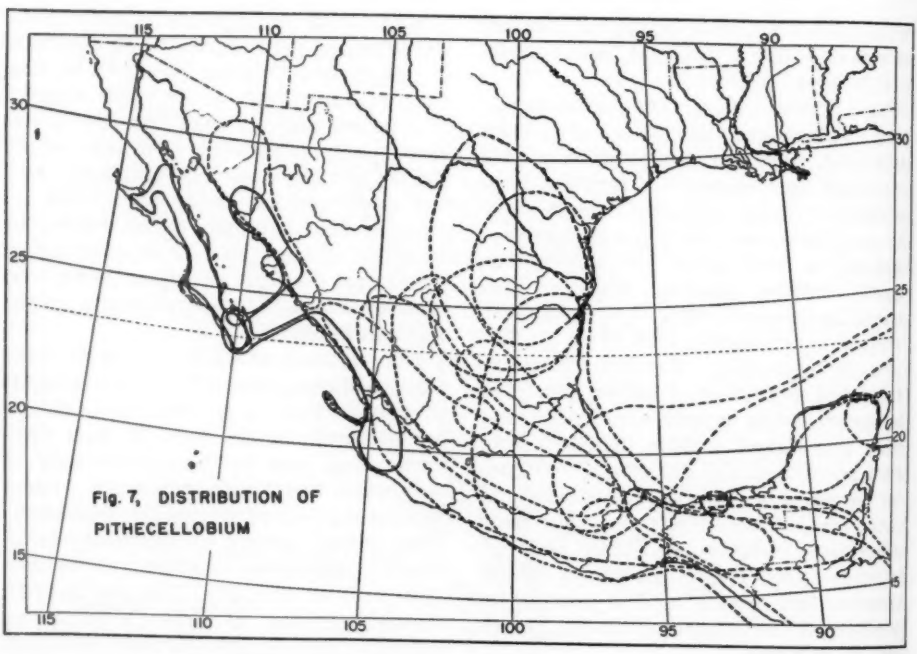

Fig. 7, DISTRIBUTION OF PITHECELLOBIUM

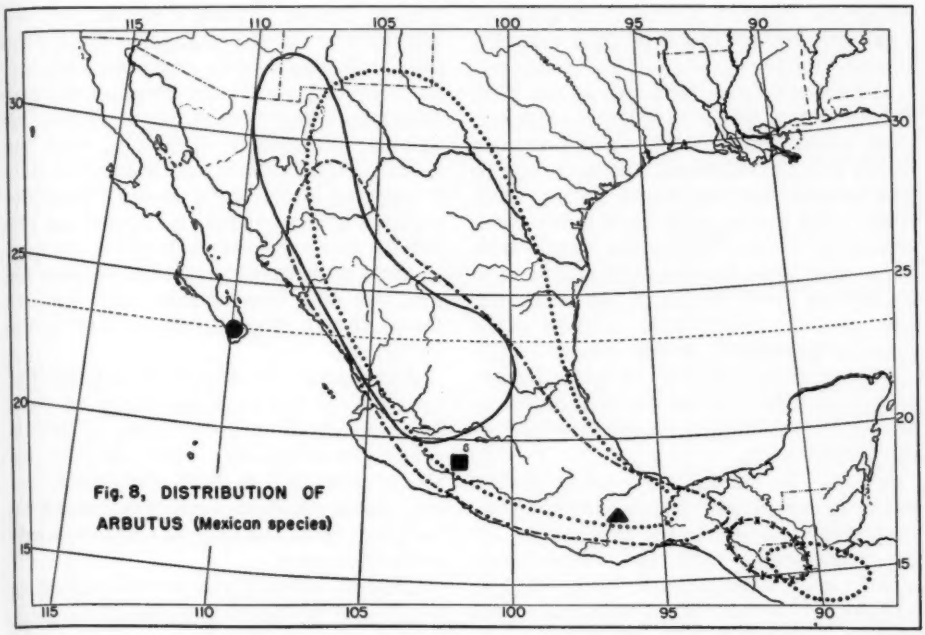

Fig. 8, DISTRIBUTION OF ARBUTUS (Mexican species)

tion in the southern Mexican lowlands, mitigates against a heavy influx of species from the moist tropics. The southern Mexican lowlands contribute so few species that the area is relatively unimportant as a source of Baja Californian plants.

Central and South American Tropics. Still fewer species found in the peninsula can be traced directly to the tropics of the western hemisphere, although there are generic relationships that may have long term significance. Prominent among these are members of the Rubiaceae, a family with a world-wide distribution in the tropics and subtropics, and represented in southern Baja California by several genera and about a score of species. Other groups that contribute to this comparatively small element include such genera as *Ficus, Passiflora, Manihot, Tillandsia, Hechtia, Hibiscus, Lantana,* and a few others. As in the case of plants migrating into the Baja California area from the tropical lowlands of southern Mexico, the desert conditions throughout most of the peninsula, and the uncertainty of summer rains in the Cape region, mitigate against a heavy representation from the American—and more distant—tropics.

Subtropical Strands. There are several families that contribute plants to the strand floras in widely separated parts of the tropical and subtropical regions of the world. Most of these are so widely distributed that it is extremely difficult to determine the centers from which they originally spread. They are well represented on the islands in the warmer parts of the Pacific Basin. Among these plants of the strand and nearby areas under strong influence of the sea are *Cocos nucifera, Scaveola plumieri, Rhizophora mangle, Avicennia nitida, Stegnosperma halimafolium,* and a few others. Incidentally, the northward extension of *Rhizophora mangle* on the two sides of the peninsula sharply illustrates the effectiveness of the isolation afforded a narrow gulf by a peninsula separating it from the colder waters of the open ocean. The

mangrove occurs as far north as Bahía de Los Angeles, by discontinuous colonies, but on the Pacific side of the peninsula it is known only as far north as the Magdalena Bay strands, a full three degrees short of the northernmost known colonies of the plant at Bahía de Los Angeles. In like manner, *Cocos* grows no farther north than Todos Santos, only a few miles north of the tip of the Cape on the Pacific side, but a few trees are producing fruit near Mulegé on the Gulf side of the peninsula. The coconut is also able to grow more than three degrees farther north on the Gulf coast than it can on the colder Pacific shore. At neither place are enough fruits produced to provide coconuts for commercial exploitation.

Weeds. In virtually all parts of the world occur plants that are aggressive, adaptable, and often able to compete all too successfully with the crops upon which man depends for food, fabrics, building materials, or medicinals. The sources of such weeds are varied, and their offspring often migrate long distances owing to their close association with man's commercial crops. Since these plants are so varied in their origin, and often so ubiquitously present, they are of little value in tracing origins of the native flora and the routes of migration followed by the native plants. Hence no further heed will be paid them.

Endemism in Baja California.

Endemism is high among the plants of Baja California. Genera that are, at our present state of knowledge, completely confined to the peninsula, include *Alvordia, Bartschella, Burragea, Behria, Clevelandia, Cochemia, Coulterella, Harfordia, Machaerocereus, Ophiocephalus, Triteleiopsis, Pachycormus,* and *Xylonogra* (Figs. 9, 10). Among these the closest relationships of *Bartschella, Cochemia,* and *Machaerocereus* are with genera on the mainland of Mexico. *Ophiocephalus* and *Clevelandia* are related to each other and to the genus *Gerardia* of the eastern United States. *Behria's* closest relative probably is on the mainland of Mexico, and *Triteleiopsis* was originally included in *Brodiaea,* a western North American genus to which it certainly is closely affiliated. *Xylonogra, Burragea,* and the more northerly *Zauschneria* seem to form a more or less natural group. Thus the endemic genera appear to have come primarily from the Sierra Madran element of the North American flora, but there are also ties with those genera that now are found chiefly if not solely farther to the north.

Bergerocactus is almost an endemic, but does have a few colonies living on Catalina Island off the southern California coast. *Viscainoa* and *Idria* likewise are almost confined to Baja California, but each has a small segment of its range extending across the Gulf of California into western Sonora.

Endemic species are far too numerous to list, and represent many families, ranging from the genus *Cupressus* in the gymnosperms and *Cheilanthes brandegei* in the ferns, to the Compositae. Some of these are well known and have been collected through a good part of the peninsula, others are still known from only one or a few isolated localities. The relationships of these endemics follow more or less that indicated in the discussion of the broader aspects of the floristic elements occurring in the various phytogeographic areas presented earlier in this paper.

Routes of Migration

Without taking into consideration the evidence that might be closely applicable if we had a few fossil floras from Baja California for comparison with those of the arid regions in California and Nevada, an assessment of the modern flora suggests that there were four main routes of migration followed by plant elements coming into the peninsula, and that numerous subsidiary routes fed into the main ones. Figure 11 depicts an attempt to indicate

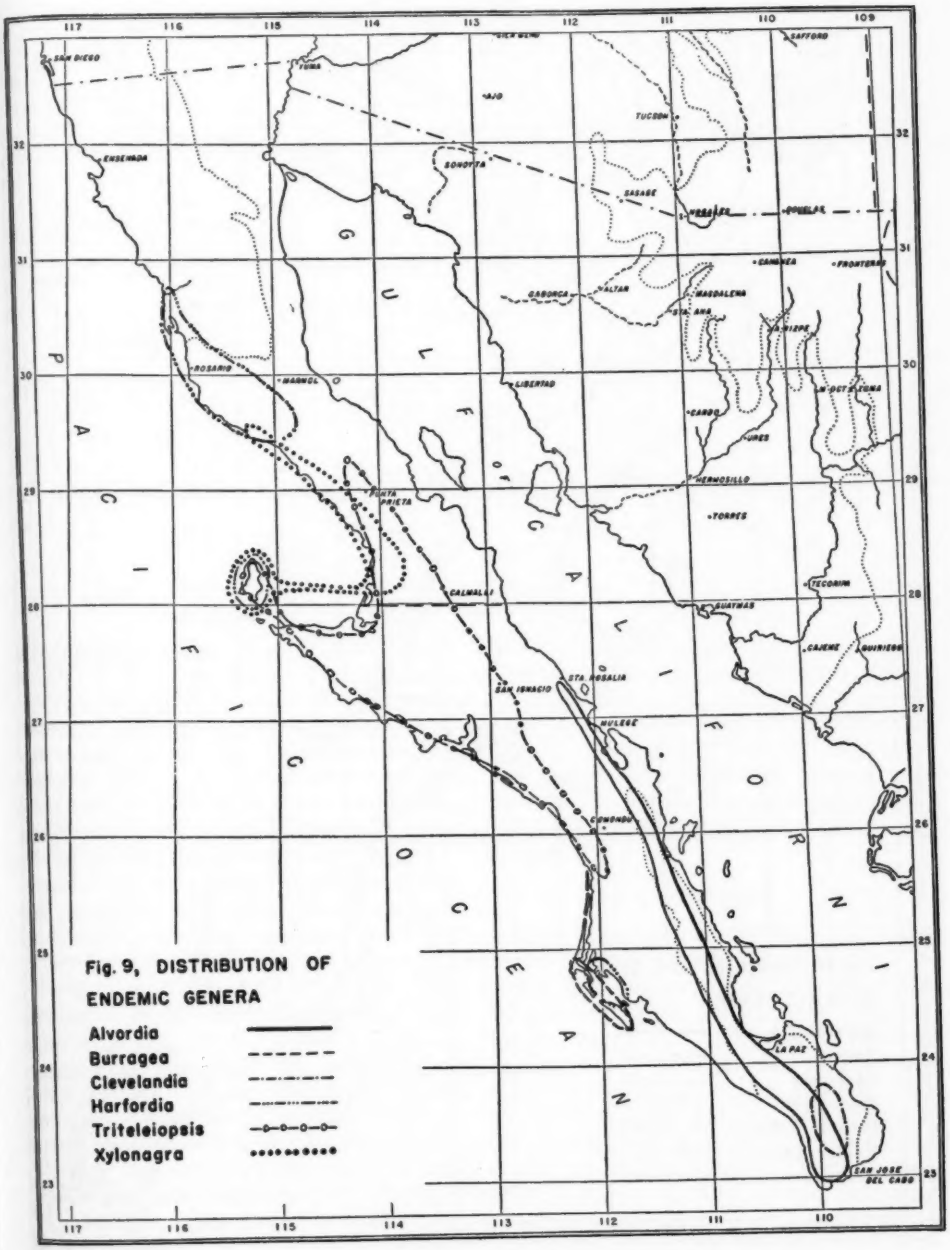
Fig. 9, DISTRIBUTION OF ENDEMIC GENERA
Alvordia
Burragea
Clevelandia
Harfordia
Triteleiopsis
Xylonagra
PACIFIC OCEAN
GULF OF CALIFORNIA
SAN DIEGO
YUMA
AJO
TUCSON
ENSENADA
SONOYTA
BASASEACHI
NOGALES
DOUGLAS
CANANEA
FRONTERAS
CABORCA
ALTAR
MAGDALENA
STA. ANA
ARIZPE
ROSARIO
MAGDALENA
LIBERTAD
CARBO
LA DIVISA
HERMOSILLO
PUNTA PRIETA
TORRES
CALMALLI
TECORIPA
GUAYMAS
CAJEME
QUIRIEGA
STA ROSALIA
SAN IGNACIO
MULEGE
GUAYMAS
LA PAZ
SAN JOSE DEL CABO
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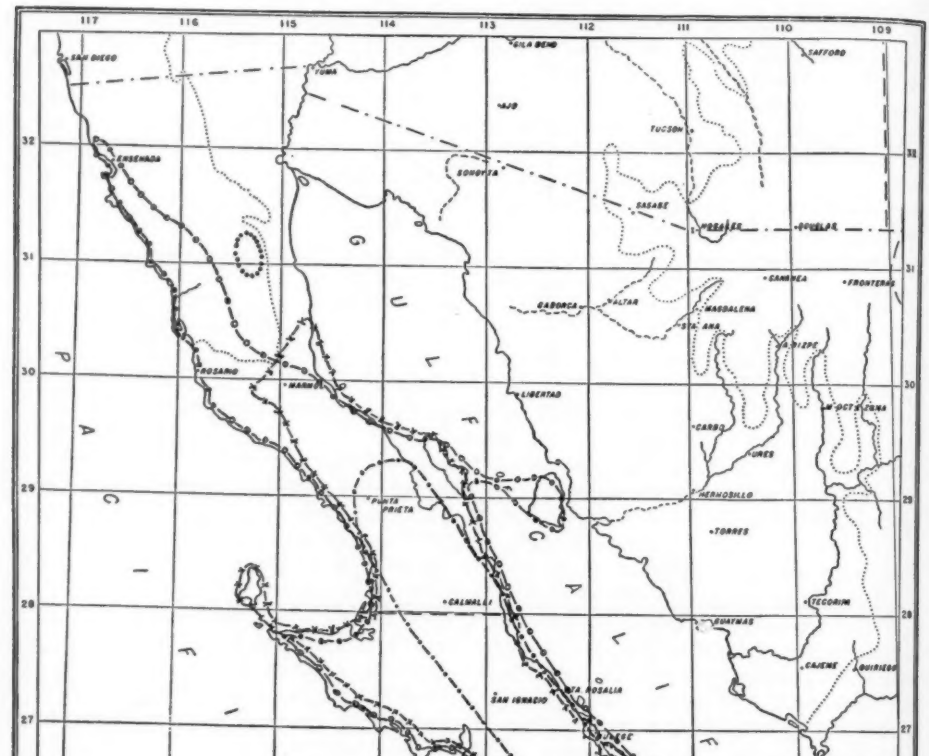
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SAN DIEGO
TIJUANA
ENSENADA
YUMA
GILA BEND
AJO
TUCSON
CAFFORD
SONOYTA
BASABE
DOUGLAS
CANANEA
FRONTERAS
GABORCA
ALTAR
MAGDALENA
STA. ANA
ARIZPE
ROSARIO
MAGDALENA
LIBERTAD
CARBO
ORES
M. OCTAVIANA
HERMOSILLO
PUNTA PRIETA
TORRES
CALMALLI
TECORIPA
GUAYMAS
CAJEME
QUIRIEGO
SAN IGNACIO
STA. ROSALIA
LORETO
GUAYMOND
LA PAZ
CABO SAN LUCAS
GULF OF CALIFORNIA
PACIFIC OCEAN
Fig. 10, DISTRIBUTION OF ENDEMIC GENERA
Bartschella
Behria
Cochemia
Coulterella
Machaerocereus
Opiocephalus
Pachycormus

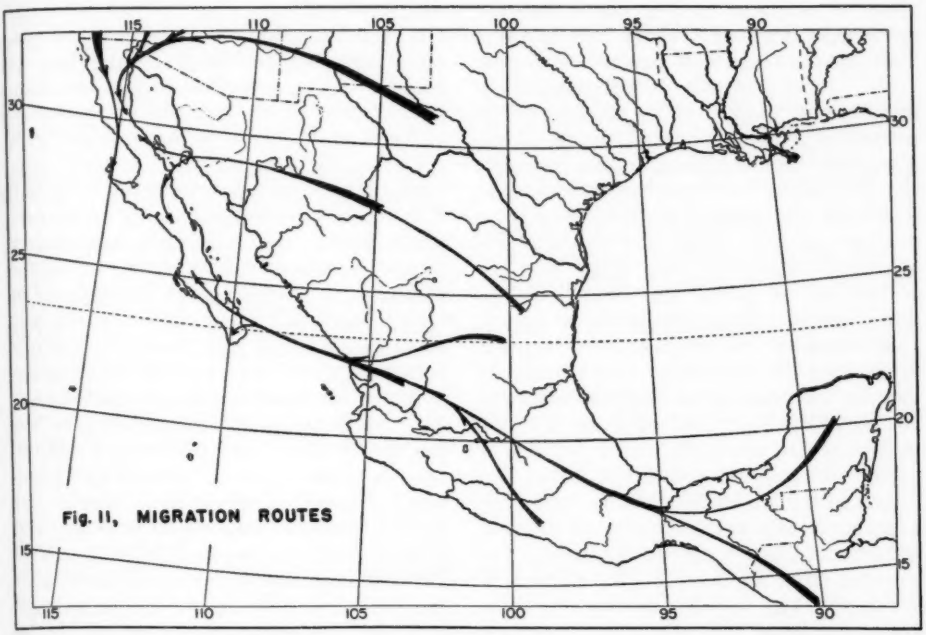

Fig. 11, MIGRATION ROUTES

diagramatically the general areas from which the evidence indicates such migrations have come. The width of the arrows does not hold significance quantitatively, but shows rather that with distance increasing from a particular center of distribution the flow falls away and fewer and fewer species manage to push outward from the home range. Only four instead of five main routes of entrance into the peninsula have been shown, because in many respects the migration from the Great Basin-Rocky Mountain area is a secondary one that joins either the Californian or the Sonoran-Chihuahuan passageway.

Questions involving the problems of "land bridges" are intriguing and interesting, but without fuller knowledge of the geological and paleontological history of the peninsula and particularly of the trough that now is occupied by the Gulf of California, speculation can be little more than just that. It is a demonstrable fact that certain plants, more or less closely related to plants on the mainland of Mexico, occur on Baja California. They got to the latter area perhaps in different ways at different times or in different ways in different parts of the peninsula. The intermingled elements present fascinating puzzles for the plant geographer and the paleobotanist to solve—or attempt to solve.

Discussion

Since it is known that the land mass constituting the peninsula of Baja California has been substantially the same for a considerable period, with only the central, lower parts subjected to flooding by sea water between the Eocene and Pliocene periods, and since there is little reason to believe that the meteorological conditions have changed very drastically during the period since the Miocene, one may be prone to think of the peninsula as presenting uniformly arid conditions to plants throughout the Tertiary. Yet paleobotanical evidence obtained a few de-

grees of latitude farther north indicate a warmer, moister climate in the early Tertiary than exists at present (Axelrod, 1948). It is probable, if not completely certain, that the aridity so pronounced at present is a phenomenon of more recent inception than is often thought, and that the peninsula was much wetter a few thousand years ago than it is now. One evidence of this, other than paleobotanical, is the comparatively large number of families of plants represented in the desert parts of Baja California by a very small number of species, even though these families contribute importantly to the physiognomy of the flora on the Sierra Madre Plateau or in moister areas still farther south. Similarly, some families of plants well represented in the Sierra Nevada and the Rocky Mountains have only a few scattered species present in the arid portions of the peninsula. Examples can be cited from among the Umbelliferae, a family that has scores of genera and hundreds of species in the temperate, wetter parts of the continent, but is represented in Baja California by only 15 genera and 20 species; from the genus *Chaenactis* which is abundantly represented in California and the Great Basin-Rocky Mountain area, but has only a few stragglers getting into Baja California; or the contrast between the large numbers of species of *Penstemon* in western North America north of the International Boundary between the United States and Mexico with the meager showing of that genus in Baja California.

Numerous additional examples could be given to show that the total vegetational cover of the peninsula draws members from a large number of families, but that among these families each contributes only one or two species to the total flora of Baja California. About 40 families are represented in Baja California by a single genus—and often by a single species only! This suggests that the adaptability of flowering plants to conditions of extreme aridity is much less than their ability to adapt to conditions of lower or higher temperatures. Perhaps it also indicates that the intrusion into the desert areas, by plants already well established in moister adjacent regions, began comparatively recently, or that the genetic plasticity of many plants is less marked with regard to adapting them to low water supplies than for other vicissitudes of living. The close phylogenetic relationships of plants living in the desert areas, with a larger number of species living at higher altitudes or farther south in regions of high rainfall, or farther north where lower temperatures and less desiccating winds occur, suggest that the right combination of genes to permit a plant to survive under conditions of low rainfall occurs less frequently than that permitting adaptation to other types of physiological tension. Nevertheless, aridity weeds out strains without these characteristics, and thereby tends to increase the rate of evolution among the few recombinants that can withstand the rigors of low rainfall and high temperatures (Stebbins, 1952).

The wonder is not so much that the peninsula of Baja California has been populated by representatives from a number of different phytogeographical areas but that such a large number of plant families has been able to produce even a few genera and species that could persist and thrive under the marginal conditions pertaining there. This ability to adapt to conditions of extreme aridity, be it by increase in succulence, early loss of leaves following the onset of drought, or by escaping drying injury by rapid production of flowers and seeds, is inherent in many different families, although in varying degrees. Such abilities and adaptations play important roles in the migrations and migration potentialities among families contiguous to an arid area in which the plant population has not yet reach equilibrium with the environmental factors operative there.

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The Entomofauna with Special Reference to its Origins and Affinities

FRED S. TRUXAL

THE FOUNDATIONS for insect faunal studies of Baja California, particularly in reference to origins and affinities, have been very poorly laid. Due to the paucity of insect fossils, we must rely chiefly on the biogeographical analysis of present-day species to postulate the past history. Any generalizations made at this time, therefore, must of necessity be purely provisional, with most of our relevant evidence being drawn from an analysis of the distribution of known centers of existing genera and their allies.

For the most part, information presented herein is the result of compilation and evaluation of previously published works. It is based primarily on winged representatives of certain families from our six largest orders of insects, the Coleoptera, Lepidoptera, Hymenoptera, Diptera, Hemiptera, and Orthoptera. Baja California, in spite of its interesting insect fauna, has been badly neglected by collectors and, therefore, the systematics of this group of animals is in the same state of neglect. All that a brief essay such as this can do, then, is to offer a point of view in regard to certain groups. The nature of this report does not allow for the citing of the many specific examples which have been previously cited in the literature.

Historical Summary of Major Field Work

As an introduction to the subject of insect biogeography that follows, a synoptic summary of some of the more important explorations which have yielded material of sufficient quantity to produce significant publications is presented below (Michelbacher and Ross, 1942).

Perhaps the first Baja California insect specimens to reach the hands of specialists were taken by J. Xantus de Vesey in 1859–1861. These were included in natural history material collected for the Smithsonian Institution. The locality given as the source of his material is Cape San Lucas (southernmost tip of peninsula), but according to Horn (1894) the specimens were probably collected between San José del Cabo and La Paz.

1888–1894: The California Academy of Sciences Expeditions. The California Academy of Sciences early recognized the need for material from Baja California and through a number of expeditions between 1888 and 1894 secured a large number of insect specimens which have helped form the basis of our knowledge of the nature of the fauna. These collections, however, were largely destroyed by the San Francisco earthquake and fire of 1906. Many of the types were saved, however. Many localities throughout the length of the peninsula were visited, as well as nearby islands.

1901: Gustav Beyer. A small but significant collection of beetles was taken in the Cape Region.

1905–1906: The California Academy of Sciences Expedition to the Galapagos Islands. A small collection was made by F. X. Williams taken on the offshore islands and at Ensenada.

1911: U.S.S. "Albatross" Expedition of the American Museum of Natural History. A small collection of insects was secured from the Cape Region.

1921: Expedition of the California Academy of Sciences to the Gulf of California. Mostly insular material was taken but a few short stops were made on the peninsula. The insect material taken contributed to the publication of several noteworthy papers.

1923: Wm. M. Mann. Collections were made in the southern portion of the peninsula.

1925: The California Academy of Sciences Expedition to the Revillagigedo Islands. Mostly insular material was taken but several short stops were made on the peninsula.

1928: T. Craig. Mostly Lepidoptera were taken from the southern shores of Baja California and nearby islands.

1930: The Newbold-Morris Expedition. An overland trip was made throughout the length of the peninsula. Mostly Orthoptera were taken.

1938: The Michelbacher-Ross Expedition. This expedition secured more material than any previous trip: approximately 50,000 insect specimens. Members of this expedition went overland throughout the entire length of the peninsula.

1938-1939: The Rindge Expeditions. Mostly Lepidoptera were taken from the southern portion. The participants traveled by boat.

1939: Ross-Michener-Folsom. Two short trips to the northern portion of the peninsula were made. A considerable number of insects were taken.

1941: The California Academy of Science Expedition to Lower California. An extensive collection was made by E. S. Ross and G. E. Bohart, who traveled overland for the entire length of the peninsula.

The Allan Hancock Foundation Expeditions, starting in 1934 and continuing through the years, have contributed a great number of important insect specimens. Travel was primarily by boat and consequently much of the material was taken near the shore.

Faunal Areas [1]

Based on information gleaned primarily from the material collected on the abovementioned expeditions and from unpublished data furnished by several individual collectors, it seems quite evident that there are at least four rather well-marked faunas in Baja California (Fig. 1). Two of these, the *Californian* and *Vancouveran,* are confined to the northern one-fourth of the peninsula and represent southern extensions of these elements from California. A third element, the *Cape Region,* confined to the southern one-fourth of the peninsula, is our richest and most ancient fauna. The fourth element, the *Sonoran,* generally speaking, consists of the central one-half of Baja California.

Affinities. The *Californian* fauna presently extends southward along the west coast of Baja California to at least the area of El Rosario and inland to, and including, the Sierra de San Pedro Mártir. It exhibits southern affinities showing a relationship with certain elements now found on the Mexican Plateau and, according to Linsley (1958b) "judging from the beetles, at least some of its affinities

[1] Terms designating the four insect faunal areas have been applied in various senses by previous authors.

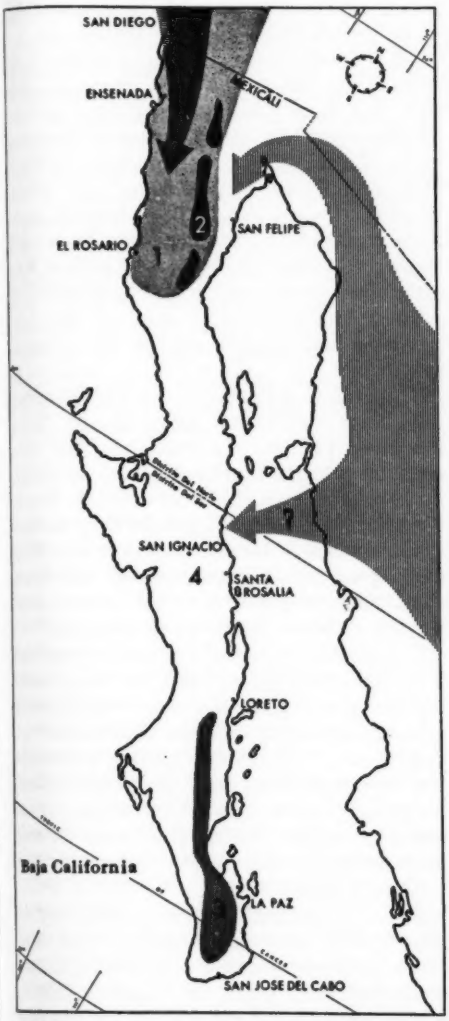

FIG. 1. Insect faunal areas and suggested dispersal routes into Baja California. (1) Californian, (2) Vancouveran, (3) Cape Region, (4) Sonoran.

suggest a closer relationship to the contemporary fauna of the arid and semi-arid west coast of South America (Peru, Galápagos, Chile, etc.) than to those of humid tropical America."

It might be noted at this point, that probably sometime during the Tertiary, a series of arid or semi-arid environments permitted the dispersal of elements between the coasts of North and South America (Linsley, 1939). At present, portions of Baja California exhibit arid phases (landward) and humid phases (seaward), the former usually characterized by desert or semi-desert conditions. Michener (1954) has pointed out that xeric communities even now exist in the vicinity of the Canal Zone in Panama. These arid phases might well have afforded north-south dispersal routes for both plants and animals.

The *Vancouveran* fauna is limited at present in Baja California to the higher regions of the Sierra de Juarez and Sierra de San Pedro Mártir. It exhibits northern affinities and includes present-day elements occurring along the Pacific border of North America southward from the Aleutian Islands. In more dilute form, elements are recognizable in the southern Rocky Mountains as well as in the high coniferous forests of southern Arizona and northern Mexico proper. At least some elements from the Vancouveran show a close affinity with those of Europe and eastern Asia.

The *Cape Region* fauna is limited to the area south of La Paz and extends northward in the higher canyons of the Sierra de la Giganta. This fauna has definite southern affinities and shows a close relationship with elements now found in the montane phases of southern Sonora and Sinaloa. It is probable that the Cape fauna is a remnant of a once more extensive biota that covered most of the peninsula but, because of ever increasing aridity, has retreated to its present state. As far as insects are concerned, the Cape Region fauna is our richest and best known in Baja California.

The largest in area, and the least known fauna, is the *Sonoran* which extends northward from the area of La Paz to approximately the southern extension of the Sierra de San Pedro Mártir and still farther northward along the Gulf of California. Elements found here have south-

ern affinities and are closely associated with the present-day arid and semi-arid Sonoran, Chihuahuan, and Sinoloan elements of Mexico proper as well as portions of southwestern United States.

Factors Contributing to Contemporary Distribution

In general, it is assumed that reconstruction of the past history of a group, whether origin or dispersal, cannot ordinarily be postulated with assurance on the sole basis of the present distributional pattern. Because of the paucity of fossils from Baja California, however, we must rely chiefly on the biogeographic analysis of living species in delving into the past history of Baja California insects. To make such an analysis, one must consider two sets of facts: first, morphological characters of the species on which phylogeny is based, and then the known geographic distribution of the species from which the dispersal pattern may be deduced (Ross, 1958).

Of the factors, past and present, which contributed to the present-day geographical distribution of the insects of Baja California, two are especially obvious. Nearly all plant-eating insects develop a high degree of specificity in their food habits. Such restrictions naturally limit the geographical ranges of the insects to the ranges of the necessary host plants. In addition, the temperature-topography restrictions further narrow insects to but a portion of that range.

As concerns past history and associations, the major migrations of western geofloras described by Axelrod (1957) are important to an understanding of present-day distribution patterns. The combination of Post-Miocene geological and climatic changes in the far west resulted in a southward movement of the Arcto-Tertiary geoflora, and a northward and northwestward movement of the Madro-Tertiary geoflora from a Mexican center of origin. A Neotropical-Tertiary geoflora retreated southward along the Pacific coast. Shifts of geographic ranges now in progress are primarily northward.

Of the four faunal areas in Baja California, the Vancouveran is the only one that has been associated with an Arcto-Tertiary geoflora and apparently had an early Holarctic derivation. The Californian and Sonoran appear to have been associated with the Madro-Tertiary geoflora and almost certainly must have had an early Neotropical origin. The Cape Region also appears to have been associated with a Madro-Tertiary geoflora but apparently had a much earlier Neotropical origin.

Insect flow responsible for the present-day Baja California entomofauna then has been primarily northward from dispersal centers in Mexico, Central America, and from at least the west coast of South America. Rehn (1958), referring to the Sonoran area of Mexico proper, states that "this great evolutionary center has been the outstanding North American center of generic differentiation for Orthoptera."

Undoubtedly the main route of dispersal into Baja California, used by the northward migrating insects, was overland and around the northern end of the Gulf of California. It is not too difficult to visualize, however, that very early trans-Gulf dispersal routes existed, particularly if one argues that during the Cenozoic era, land bridged what is now known as the Gulf of California.

Age. An analysis of the morphology of present-day material suggests that the Cape Region contains our oldest fauna from the standpoint of time of origin, while the Sonoran appears to contain our most recent; the Californian and Vancouveran faunas seem to be intermediate in time of origin. Paleogeographic interpretations seem to lend credence to these assumptions.

Endemism

For the most part, endemism on both the generic and specific level in Baja California is limited to the Cape Region. En-

demic genera and species are recorded, however, from all four faunal areas. Endemism on the species level in the Sonoran fauna at present is relatively high but the writer feels that it is, for the most part, an artificial endemism that will disappear with more conscientious collecting on the Mexican mainland. It is interesting to note, however, that as far as the flightless insects are concerned, particularly in reference to certain members of the families Tenebrionidae and Curculionidae, the occurrence of endemism does not fit the pattern just mentioned. In these two groups, at least, there are more endemic genera and species recorded for the Sonoran fauna.

Non-Insect Arthropods

It is interesting to note that another group of terrestrial arthropods, the Araneida or spiders, exhibit somewhat the same distribution pattern in Baja California as has been shown for the insects. In the words of Chamberlin (1924): "The spider fauna of the Gulf of California region is complex, and is undoubtedly diverse in origin, both as to the time and sources of derivation of its various groups and elements. This large group presents not one, but many problems of origin and distribution; for adequate solution of these problems, extensive and accurate work must be done on the arachnids of various other regions. This fauna, in the main, has been long established, as indicated by the large percentage of forms peculiar to the area, or extending but little beyond it, nearly two-thirds of the known species and many genera falling in this category. The section seems to have been the center of origin for, or the highway for, the various forms that have penetrated into the southwestern United States. The reverse movement of peculiarly North American forms has apparently been much more restricted, and one gets the impression from the affinities of the indigenous species and genera, that so far as the more primitive and peculiar spider fauna is concerned, the Gulf of California area is tropical, an extension, as it were, of South America."

Discontinuous Distribution. To illustrate a pattern of discontinuous distribution which is found in many of the spiders of Baja California, the genera *Megamyrmecion, Zimiris,* and *Chorizomma* will serve as good examples. *Megamyrmecion,* which is represented by several species in California and the Gulf of California area, is known elsewhere in the Americas only in Chile. This genus, however, also occurs in the desert regions of Africa and in Madagascar and India. *Zimiris,* which is represented by at least one species in the Cape Region of Baja California, is known elsewhere only from southern Arabia and from India. The genus *Chorizomma* exhibits an interesting pattern of distribution. Of this genus, two species are known from California and Baja California while elsewhere it is known only from southern France and in Spain. This is one of many similar cases afforded by diverse groups of organisms in which forms from the Pacific coast of North America have their closest relatives in western Europe.

Summary

The most pertinent generalizations and assumptions that can be made from the synthesis of available data are as follows:

First, the peninsula of Baja California can be roughly divided into four faunal areas: two of these, the Californian and Vancouveran are confined to the northern one-fourth of the peninsula and represent southern extensions of these elements in California. A third element, the Cape Region, confined to the southern one-fourth of Baja California, is our richest fauna and oldest from the standpoint of time of origin. The fourth element, the Sonoran, generally speaking is contained in the central one-half of the peninsula.

Second, all Baja California faunas exhibit southern affinities and derivations except the Vancouveran which shows northern affinities. Insect flow was pri-

marily, then, northward from Mexico, Central, and South America.

Third, the seemingly most important factors influencing contemporary distribution of the entomofauna are: restrictions enforced in the past and present by the flora of Baja California and the climatic and topographical fluctuations from the Miocene through the Pleistocene—or one might even say—to the present.

Fourth, for the most part, endemism on the generic level in Baja California is limited to the Cape Region with the Sonoran area ranking second.

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An Analysis of the Recent Land Mammals

ROBERT T. ORR

GEOLOGICAL EVIDENCE indicates that the peninsula of Baja California has not changed greatly since the early Pliocene apart from the elevation of the Magdalena Plain, siltation at the head of the Gulf of California, resulting in a broader land bridge with the Sonoran Desert of the mainland, and probably the appearance of more coastal islands. The Gulf, consequently, has served as an effective barrier to the free movement of most land mammals between the peninsula and the mainland of Mexico. It is not surprising, therefore, that the great majority of land mammals presently inhabiting this region appear to be of northern origin. According to Hershkovitz's (1958) classification, all of the 50 native mammalian genera here recognized as being represented in Baja California occur in the Holarctic or Nearctic region. Twenty-two of these genera are strictly Holarctic or Nearctic while the remaining 28 also occur in the Neotropical Region.

The mammalian fauna of Baja California, likewise, exhibits a high degree of endemism. Over 25% of the species occurring there today can be classified as endemics. The geographical isolation just referred to has been partly responsible for this. Of great importance, however, have been the various climatic changes that have occurred in this region since the Late Tertiary. Much of our knowledge of these changes is a result of studies made on the geoflora.

According to Axelrod (1958) there was a gradual increase in aridity in western North America from the Early Pliocene to the Quaternary which resulted in a southward movement of the Madro-Tertiary Flora. In Baja California at present remnants of this flora consisting of oak woodland and arid thorn scrub are found in the Cape Region. The increase in aridity was also responsible for the development of the present desert in western North America which is of late Cenozoic age. The desert regions of Baja California, however, were greatly affected during the Pleistocene as a result of climatic fluctuations between the glacial and interglacial periods. It is likely that during periods of glacial maximum there was essentially no desert in Baja California. At such times the invasion of the peninsula by certain northern and montane species was no doubt correlated with the southward movement of the Arcto-Tertiary Flora.

These climatic fluctuations must have caused altitudinal as well as northward and southward movements of many species. With an increase in temperature and aridity in post-glacial times, the general movement of many mammals that were of widespread distribution in the lowland areas during the periods of glacial maximum was either northward or to higher elevations or both. This would account for the ecologic isolation that we find in certain groups of mammals on the peninsula today. In some instances this isolation has only resulted in subspecific differentiation whereas in others full species have developed from parent stocks now existing farther to the north.

The post-glacial expansion of desert in Baja California has also been responsible for its relatively recent invasion by species from the northeast. These factors account for the presence of a richer ter-

restrial mammalian fauna in the northern part of the peninsula than in the central desert and Cape Region.

More than half of the endemic species of land mammals in this region are restricted to islands. A number of these so-called species, however, are merely spatially isolated populations that differ only slightly from species found on the main body of the peninsula.

For convenience in the present discussion, 97 named species of native land mammals are recognized as occurring in the Baja California region in recent times. It will be pointed out that some of these species are questionable, but no attempt will be made here to change their status.

In order to analyze the origin of the land mammals, each species has been placed in one of six major categories. These categories indicate geographical affinities, and the assignment of a species to a particular category has in some instances of necessity been a rather arbitrary one. The six categories referred to are as follows: (1), species widespread over North America; (2), species occurring over much of western North America; (3), Pacific coastal species; (4), species primarily of southwestern United States and northern Mexico; (5), species primarily of the Mexican mainland; (6), species endemic or essentially endemic to Baja California.

Species Widespread over North America

The following 16 species occurring in Baja California are also widely distributed over many other parts of North America:

Small-footed myotis (*Myotis subulatus*)
Big brown bat (*Eptesicus fuscus*)
Red bat (*Lasiurus borealis*)
Townsend's big-eared bat (*Plecotus townsendii*)
Brazilian free-tailed bat (*Tadarida brasiliensis*)
Deer mouse (*Peromyscus maniculatus*)
Hispid cotton rat (*Sigmodon hispidus*)
Muskrat (*Ondatra zibethica*)
Coyote (*Canis latrans*)
Gray fox (*Urocyon cinereoargenteus*)
Raccoon (*Procyon lotor*)
Badger (*Taxidea taxus*)
Spotted skunk (*Spilogale putorius*)
Striped skunk (*Mephitis mephitis*)
Mountain lion (*Felis concolor*)
Bobcat (*Lynx rufus*)

It is interesting to note that of these 16 species five are bats, eight are carnivores, and the remaining three are rodents. Considering the latter, only the deer mouse (*Peromyscus maniculatus*) is truly represented on the peninsula. The hispid cotton rat (*Sigmodon hispidus*) and the muskrat (*Ondatra zibethica*) follow the shore line of the Colorado River; their presence in the extreme northeast part of the peninsula is merely a political accident. If the Sonoran boundary were moved a mile westward, these two species would not be included in the Baja California fauna. Although the beaver (*Castor canadensis*) has not been recorded on the peninsula, it has been taken along the Sonoran side of the Colorado River and there is little reason to believe that a beaver will not swim across a river. Like the cotton rat and the muskrat, however, the beaver will never be truly a part of the fauna of Baja California.

It is obvious that most of the species on this list are tolerant to widely varying climatic conditions. For example, in California alone the deer mouse, the coyote, the badger, the mountain lion, and the bobcat have all been recorded from sea level to well over 10,000 feet.

Species That Occur Over Much of Western North America

The following 24 species are broadly limited to western North America.

Yuma myotis (*Myotis yumanensis*)
Long-eared myotis (*Myotis evotis*)
Long-legged myotis (*Myotis volans*)
California myotis (*Myotis californicus*)
Western pipistrelle (*Pipistrellus hesperus*
Pallid bat (*Antrozous pallidus*)
Desert cottontail (*Sylvilagus audubonii*)
Black-tailed jack rabbit (*Lepus californicus*)
White-tailed antelope ground squirrel (*Ammospermophilus leucurus*)

Southern pocket gopher (*Thomomys umbrinus*)
Little pocket mouse (*Perognathus longimembris*)
Long-tailed pocket mouse (*Perognathus formosus*)
Merriam's kangaroo rat (*Dipodomys merriami*)
Western harvest mouse (*Reithrodontomys megalotis*)
Canyon mouse (*Peromyscus crinitus*)
Brush mouse (*Peromyscus boylii*)
Piñon mouse (*Peromyscus truei*)
Desert wood rat (*Neotoma lepida*)
Kit fox (*Vulpes macrotis*)
Grizzly bear (*Ursus horribilis*)
Ringtail (*Bassariscus astutus*)
Mule deer (*Odocoileus hemionus*)
Pronghorn (*Antilocapra americana*)
Mountain sheep (*Ovis canadensis*)

Apart from the endemics, this category contains the greatest number of species, including six bats, two lagomorphs, ten rodents, three carnivores, and three artiodactyls. This is not surprising when we consider that these are species primarily adapted to the arid parts of western North America and that Baja California today is largely desert. As would be expected, therefore, most of these species are rather widely distributed over the peninsula. There are, however, exceptions. The grizzly bear, which is now extinct in Baja California, occurred within historic times only in the woodland and chaparral-covered areas of the northwest.

The present range of the piñon mouse in Baja California merits comment because of its bearing on past distributional patterns. At present the species occurs in the Sierra Juárez and the Sierra San Pedro Mártir in the northern Montane Region and also in the Cape Region in the Laguna and Victoria mountains. The population in the Cape Region (*Peromyscus truei lagunae*) is recognized as subspecifically distinct from *Peromyscus truei martirensis* occurring many hundreds of miles to the north. Hoffmeister (1951) in his study of this group of mice comments on the nearer relationship of the Cape Region population to that of *Peromyscus truei gentilis* of the Sierra Madre Occidental of Mexico rather than to *P. t. martirensis* to the north. The possibility of trans-gulf invasion, however, is not seriously considered. Instead that author suggests that this probably is an example of parallel evolution. Davis (1959: 82), commenting on this same problem, suggests that "An equally valid hypothesis is that *lagunae* has been derived from a *gentilis*-like ancestral population which followed the Madro-Tertiary flora from northern Mexico to the Cape District." This seems likely in view of the fact that the oak woodland in the highlands of the Cape Region as well as the arid thorn scrub of the lowlands is a remnant of the Madro-Tertiary Flora which once extended north into western United States. Between the Cape Region and the northern chaparral woodland of the peninsula there is presently a great expanse of desert unsuitable for habitation by *Peromyscus truei*.

Pacific Coastal Species

The third category, Pacific coastal species, comprises two insectivores, one lagomorph, and eight rodents or a total of 11 species as follows:

Ornate shrew (*Sorex ornatus*)
Broad-footed mole (*Scapanus latimanus*)
Brush rabbit (*Sylvilagus bachmani*)
Merriam's chipmunk (*Eutamias merriami*)
California ground squirrel (*Spermophilus beecheyi*)
Chickaree (*Tamiasciurus douglasii*)
California pocket mouse (*Perognathus californicus*)
Agile kangaroo rat (*Dipodomys agilis*)
California mouse (*Peromyscus californicus*)
Dusky-footed wood rat (*Neotoma fuscipes*)
California vole (*Microtus californicus*)

These are species whose ranges are confined to the Pacific coastal region of western North America. For the most part they enter only the northern part of the peninsula either in what Nelson (1921) refers to as the San Diegan District which extends southward along the west coast to the vicinity of El Rosario or in

the Montane Region which includes the Sierra Juárez and Sierra San Pedro Mártir immediately to the east of the San Diegan District.

There is considerable variation in the present north-south distribution of these species. The brush rabbit (*Sylvilagus bachmani*), for example, ranges from northwestern Oregon south to the Cape Region of Baja California. By way of contrast, the agile kangaroo rat (*Dipodomys agilis*) is limited to southwestern California and northwestern Baja California and could almost be placed in the endemic list. The chickaree (*Tamiasciurus douglasii*) ranges from southern British Columbia south to northern Baja California. At the southern end of its range, however, its distribution is discontinuous. Chickarees are absent between the southern end of the Sierra Nevada in California and the Sierra San Pedro Mártir. They do not occur in the coniferous forests on the high ranges of southern California or even in the Sierra Juárez.

Two species in this group have a discontinuous distribution on the peninsula. The most notable is the ornate shrew (*Sorex ornatus*) which ranges from northern California south to northern Baja California, and is also found in the Sierra de la Laguna of the Cape Region. The population found in the latter area represents a distinct race, *Sorex ornatus lagunae*, moreover, it is ecologically isolated by many hundreds of miles from the range of the species to the north. Like the piñon mouse (*Peromyscus truei*), this species appears once to have ranged widely over the peninsula when more temperate conditions prevailed but increased aridity produced the present discontinuous distributional pattern. A separate species, *Sorex juncensis*, has been described from Socorro, 15 miles south of San Quintín in the northern part of the peninsula. Although it is here considered under endemic species it is closely related to *Sorex ornatus* and may prove to be conspecific.

Another interesting distributional pattern is shown by the Merriam's chipmunk (*Eutamias merriami*) which occurs in the higher parts of the Sierra Juárez and Sierra San Pedro Mártir and then is found in the area immediately north of San Ignacio. The latter population lives far from the coniferous forest and chaparral type of habitat frequented by members of this species in northern Baja California and in the coast ranges and Sierra Nevada of California. Undoubtedly *Eutamias merriami*, like *Sorex ornatus* and *Peromyscus truei*, once had a much more extensive and continuous distribution in this region when more temperate climatic conditions prevailed.

Species Primarily of Southwestern United States and Northern Mexico

The fourth category includes those species that are primarily of southwestern United States and northern Mexico. This group consists of one shrew, one bat, and seven rodents as follows:

- Crawford's desert shrew (*Notiosorex crawfordi*)
- California leaf-nosed bat (*Macrotus californicus*)
- Round-tailed ground squirrel (*Spermophilus tereticaudus*)
- Bailey's pocket mouse (*Perognathus baileyi*)
- Desert pocket mouse (*Perognathus penicillatus*)
- Desert kangaroo rat (*Dipodomys deserti*)
- Cactus mouse (*Peromyscus eremicus*)
- Southern grasshopper mouse (*Onychomys torridus*)
- White-throated wood rat (*Neotoma albigula*)

The desert shrew has been taken at widely separated localities over the peninsula. The same is true of the leaf-nosed bat, Bailey's pocket mouse, and the cactus mouse. Four of the species in this group, however, are strictly limited to the arid northeastern section which represents a southern extension of the Colorado desert. These are the round-tailed ground squirrel, the desert pocket mouse, the

desert kangaroo rat, and the white-throated wood rat.

Species Primarily of the Mexican Mainland

Peters' bat (*Balantiopteryx plicata*)
Peters' leaf-chinned bat (*Mormoops megalophylla*)
Mexican long-tongued bat (*Choeronycteris mexicana*)
Long-nosed bat (*Leptonycteris nivalis*)
Mexican funnel-eared bat (*Natalus mexicanus*)
Cave myotis (*Myotis velifer*)
Southern yellow bat (*Dasypterus ega*)
Pocketed free-tailed bat (*Tadarida femorosacca*)
Big free-tailed bat (*Tadarida molossa*)

The nine species that are placed in this category are all bats. The cave myotis (*Myotis velifer*) has the most extensive range, occurring in parts of southwestern United States as well as throughout most of Mexico. Although it occurs in the Colorado desert of southeastern California it has been taken in Baja California only in the Cape Region where it is represented by the race *M. v. peninsularis*.

Several species, including Peters' bat (*Balantiopteryx plicata*), Peters' leaf-chinned bat (*Mormoops megalophylla*), and the Mexican funnel-eared bat (*Natalus mexicanus*) are, so far as known, restricted on the peninsula to the Cape Region. It is quite possible that they represent relatively recent trans-gulf immigrants. Climatic conditions on the peninsula during the last glacial period in North America were probably not suitable for these bats of the arid tropical zone. Even today their northern distribution is limited. Neither *Balantiopteryx* nor *Natalus* get into the United States while the range of *Mormoops* barely enters southern Texas. Significant also is the fact that no one so far has found the Baja California populations of these three species sufficiently different from the adjacent mainland populations to warrant separate subspecific names.

Endemic Species

This category includes all of those so-called species that have evolved in and are essentially unique to the Baja California region. They are as follows:

Tule shrew (*Sorex juncensis*)
Miller's myotis (*Myotis milleri*)
Fish-eating bat (*Pizonyx vivesi*)
Brush rabbit (*Sylvilagus mansuetus*)
Black jack rabbit (*Lepus insularis*)
Espíritu Santo Island antelope ground squirrel (*Ammospermophilus insularis*)
Baja California rock squirrel (*Spermophilus atricapillus*)
Little desert pocket mouse (*Perognathus arenarius*)
San Diego pocket mouse (*Perognathus fallax*)
Anthony's pocket mouse (*Perognathus anthonyi*)
Spiny pocket mouse (*Perognathus spinatus*)
Santa Catarina kangaroo rat (*Dipodomys paralius*)
Baja California kangaroo rat (*Dipodomys peninsularis*)
San Quintín kangaroo rat (*Dipodomys gravipes*)
San José Island kangaroo rat (*Dipodomys insularis*)
Margarita Island kangaroo rat (*Dipodomys margaritae*)
Baja California rice rat (*Oryzomys peninsulae*)
False Canyon mouse (*Peromyscus pseudocrinitus*)
Burt's deer mouse (*Peromyscus caniceps*)
Angel Island mouse (*Peromyscus guardia*)
Dickey's deer mouse (*Peromyscus dickeyi*)
San Estéban Island mouse (*Peromyscus stephani*)
Santa Cruz Island mouse (*Peromyscus sejugis*)
Slevin's mouse (*Peromyscus slevini*)
Bryant's wood rat (*Neotoma bryanti*)
Anthony's wood rat (*Neotoma anthonyi*)
San Martín Island wood rat (*Neotoma martinensis*)
Bunker's wood rat (*Neotoma bunkeri*)

Twenty-eight kinds of mammals are listed here under the category of endemics and of this number 23 are rodents. Three of the listed forms, however, are not strictly endemic since their ranges are not entirely limited to Baja California.

The first of these three is the fish-eating bat (*Pizonyx vivesi*). This unique bat belongs to a monotypic genus rather closely related to the genus *Myotis*. The known range of the genus and species is given by Reeder and Norris (1954: 83) as "The Coast of Sonora from the head of the Gulf of California south to Guaymas; islands of the Gulf of California from Isla San Jorge in the north to Isla San Pedro Nolasco in the south; east coast of Baja California from Bahía San Francisquito to Bahía de Los Angeles; the western coast of Baja California in the vicinity of Puerto San Bartolomé." The preference of this species for arid offshore islands in the Gulf of California makes it appear likely that it originated in this general region. So far it has not been collected south of 27° 30′ N. Lat. Like the cirio (*Idria columnaris*) and the elephant tree (*Pachycormus discolor*) this bat is primarily a peninsular species that also occurs to a limited extent in coastal Sonora. For these reasons, therefore, it is here included as an endemic.

The other two species whose ranges are not exclusively limited to within the political boundaries of Baja California but which are considered as essentially endemic to this region are the San Diego pocket mouse (*Perognathus fallax*) and the spiny pocket mouse (*Perognathus spinatus*). The former species ranges from southwestern California south to San Bartolomé Bay. As far as north-south distribution is concerned, almost three-fourths of the range of this species is within the boundary of Baja California. The spiny pocket mouse ranges from the Colorado desert of southeastern California south over much of the peninsula to the Cape Region. Both of these species must have been limited entirely to the peninsula when climatic conditions were slightly colder.

At least two of the so-called endemic species will in all probability ultimately be reduced to subspecific status at most. These are the tule shrew (*Sorex juncensis*) and Miller's myotis (*Myotis milleri*). *Sorex juncensis* was described on the basis of two specimens from Socorro, 15 miles south of San Quintín. Jackson (1928: 172) in his review of American long-tailed shrews acknowledges that additional material may show that this species and *Sorex ornatus* are conspecific. The characters distinguishing them are of no more than subspecific value. *Myotis milleri* appears to be no more than a race of *Myotis evotis*.

The two endemic lagomorphs, *Sylvilagus mansuetus* of San José Island and *Lepus insularis* of Espíritu Santo Island, are both insular species closely related to species that range widely over the peninsula. *Sylvilagus mansuetus* appears obviously to have been derived from *S. bachmani* and *Lepus insularis* from *L. californicus*. Extrinsic spatial isolation as defined by Brown (1959: 81), seems here to be the factor responsible for this specific or near specific differentiation. The expression "near specific differentiation" is used because it seems highly probable that if the natural barrier of water separating each of these insular populations from their closely related peninsular populations were not present each would freely interbreed with the parent stock. This, however, cannot be proved, at least under natural conditions.

The remaining 21 so-called endemics are all rodents. Most of these appear to have been derived from species that have invaded the peninsula from the north and subsequently become isolated spatially or ecologically. Davis (1959) has come to essentially the same conclusion regarding the birds of the Cape region. One possible exception, however, is seen in the Baja California rice rat (*Oryzomys peninsulae*). This species is confined to the Cape Region and is most nearly related to *Oryzomys couesi* (see Goldman, 1918: 46–47), a species that ranges as far north in Mexico as southern Sonora. No representatives of this genus are known north of the Cape Region on the peninsula nor in southwestern United States. There is the possibility, therefore, that acci-

dental trans-gulf crossing may account for this unusual distributional pattern. Members of this genus have invaded a number of insular areas, including the Galápagos Islands, and *Oryzomys nelsoni*, another close relative of *O. couesi*, is known from María Madre Island of the Tres Marías group off the coast of Nayarit, Mexico.

The greatest amount of endemism is seen in the genus *Peromyscus* which has seven well-defined species limited to Baja California. These species are all insular forms occurring in the Gulf of California. Five of these species, *Peromyscus pseudocrinitus, caniceps, dickeyi, stephani,* and *slevini* are confined to single islands. *Peromyscus sejugis* occurs both on Santa Cruz Island and nearby San Diego Island. Although Burt (1932: 171) in his original description of this species noted that the San Diego Island population differed slightly from that of Santa Cruz Island he did not feel that a separate subspecific name for the former was warranted.

Peromyscus guardia, on the other hand, occurs on three different islands: Mejía Island, Ángel de la Guardia Island, and South San Lorenzo Island. These islands are arranged in the form of a chain extending in a north-south direction and each has a separate subspecific population of mice.

Four insular species of wood rats have been recognized. Three are found on islands along the west coast of Baja California. These are *Neotoma anthonyi* from Todos Santos Island, *Neotoma martinensis* from San Martín Island, and *Neotoma bryanti* from Cedros Island. All three are believed to have been derived from *Neotoma lepida*, a species that occurs over much of western North America including the entire peninsula of Baja California. The fourth insular species of wood rat, *Neotoma bunkeri*, occurs on Coronados Island in the Gulf at Latitude 26° 06′ N. When first described by Burt (1932: 181) *N. bunkeri* was thought to be a member of the *fuscipes* group, a Pacific coastal species that enters the northwestern part of the peninsula. Later studies by Burt and Barkalow (1942: 290) revealed that it too is a member of the *N. lepida* group.

Nine of the endemic species of mammals are rodents belonging to the family Heteromyidae. Four of these are pocket mice of the genus *Perognathus* and five are kangaroo rats. Two of the pocket mice, *P. fallax* and *P. spinatus*, have already been discussed. A third species, *P. anthonyi*, is an insular member of the *fallax* group restricted to Cedros Island. The fourth species of pocket mouse *Perognathus arenarius* occurs over most of the arid lowlands of the peninsula from San Quintín in the northwest and Laguna Salada in the northeast south to La Paz. It is believed to be related to *Perognathus penicillatus* but occurs sympatrically with this species in the San Felipe desert region with seemingly no indication of hybridization.

Two of the kangaroo rats, *Dipodomys insularis* of San José Island and *D. margaritae* of Margarita Island, are insular forms of the wide ranging species, *Dipodomys merriami*. *Dipodomys paralius* is related to the Pacific coastal species, *D. agilis*, but the two species are sympatric. Although *Dipodomys peninsularis* has been considered as a geographic race of *agilis* by some mammalogists, Huey (1951) raised it to specific rank.

Dipodomys gravipes represents an interesting relict species belonging to the *heermani* group of central and northern California. Obviously a derivative of this group of broad-faced kangaroo rats but now separated from its nearest relatives by several hundred miles, *Dipodomys heermanni* evidently once ranged much farther south into the area presently occupied by members of the *agilis* group.

The remaining two endemic species are squirrels. The Espíritu Santo Island antelope ground squirrel (*Ammospermophilus insularis*) is, according to Howell (1938: 151), an insular form of the white-tailed antelope ground squirrel

(*Ammospermophilus leucurus*) to which it is closely allied. The Baja California rock squirrel (*Spermophilus atricapillus*) bears somewhat the same relationship to *Spermophilus beecheyi* that *Dipodomys gravipes* does to *D. heermanni*. The evidence indicates that the range of *Spermophilus beecheyi* once extended considerably farther south on the peninsula. As the climate became warmer this squirrel gradually retrenched to the north, leaving an isolated population on the lava-covered plateau extending from the Sierra San Francisco to the Sierra de la Giganta. The Vizcaíno Desert presently forms an ecologic barrier separating these two species.

Thus of the 28 so-called endemic species of land mammals found in the Baja California region, 17 represent island populations, some of them closely related to existing species present on the adjacent peninsula. Only one species, the rice rat, is distinctive of the Cape Region. Of the remaining 10 species two are believed to merit no more than subspecific rank. Most of the remaining eight species appear to be more or less well differentiated peninsular forms, some of which have obviously developed as a result of ecologic isolation.

Subspecific Differentiation

Perhaps of greater significance than the endemic species just considered are the more than 150 geographic races of land mammals whose ranges are confined entirely to the Baja California region. Forty-seven of these are insular races belonging to eight genera as follows: *Lepus*, 2; *Sylvilagus*, 1; *Thomomys*, 1; *Perognathus*, 14; *Peromyscus*, 19; *Neotoma*, 7; *Bassariscus*, 2; *Odocoileus*, 1. In addition to the more than 100 remaining subspecies that are strictly limited to the mainland of the peninsula there are a number of races whose ranges extend into the northern part of Baja California from southern California.

Actually the major centers of mammalian differentiation on the mainland of Baja California are the San Diegan District in the northwest, already referred to, the Colorado Desert District in the northeast, the Northern Montane District, the Vizcaíno Desert District and the Cape District. These are outlined by Nelson (1921, Pl. 31).

The San Diegan District is a southward extension of the faunal and floral elements that are characteristic of coastal southern California. It is a region that is relatively cool and moist as a result of prevailing westerly winds coming in from the Pacific and summer fog. It marks the southern end of the range of several species and is an area in which a number of geographic races have become differentiated. The Colorado Desert District extends southward from California on the Gulf side of the peninsula to the region of Bahía de Los Angeles. It is a region of extreme aridity and is a center of development of a number of extremely pale geographic races. Like the San Diegan District, it also marks the southern end of the range of several species of mammals. Since the boreal elements of the Sierra Juárez and the Sierra San Pedro Mártir ranges are not only separated from one another but also from those of the mountains of southern California it is not surprising that we find a number of geographic races differentiated here.

All three of these districts, however, are really southern extensions of biotic areas present in southern California. Unique to Baja California is the Vizcaíno Desert District where a great many endemic mammalian races are to be found. This likewise serves as a barrier separating certain elements in the Cape District from those in the northern part of the peninsula as has already been noted.

The Cape District, as outlined by Nelson (1921), includes a large part of the southern half of the peninsula. From the standpoint of mammalian distribution this arid tropical region could be divided into several subdistricts including the Mag-

dalena Plain, the interior lava-covered plateau, volcanic mountains such as the Sierra de la Giganta, and the high mountains near the tip of the peninsula south of La Paz.

Conclusion

In conclusion, therefore, the land mammals of Baja California appear to be largely of northern origin with a few species of bats and one rodent as possible exceptions. This seems to be the result of long separation, as far as mammalian speciation is concerned, of the main body of the peninsula from the North American continent. A rather high degree of endemism is found in the Baja California region partly as a result of this geographic separation. Equally important, however, have been the climatic fluctuations which have permitted northward and southward movements resulting in the ecologic isolation of populations of certain species. In some instances this isolation has been sufficiently long to permit specific differentiation. Insular or spatial isolation has also been a major factor influencing endemism on both the specific and subspecific level.

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The Composition and Origin of the Avifauna

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FROM THE standpoint of systematics, the avifauna of Baja California is probably better known than all of the other vertebrate faunas populating this peninsula. The attention of ornithologists has been focused on this particular avi-

fauna for approximately 60 years. Field parties from various scientific institutions have sampled the avian populations from one end of the peninsula to the other, and as a result, excellent comparative series of skins are available today in many of the museums and universities of the United States and Mexico, as well as those of Europe.

In considering the avian composition of any given area of the northern hemisphere, we are immediately confronted with the migratory species which periodically flow down over the region and then withdraw like a receding tide. This condition is naturally applicable to Baja California, and a large segment of the avifauna of the peninsula can be classed as purely migratory.

Eighteen of the 27 currently recognized avian orders of the world are represented on the peninsula and these are the same 18 shared with the United States. The entire New World embraces but 20 orders —the remaining two being purely neotropical—the Rheiformes or Rheas of South America and the Tinamiformes or Tinamou which range through the neotropical region from the Mexican mainland to southern South America. Of the 59 families known to occur in Baja California, 47 are resident and 12 are purely migratory. Within these 59 families are some 352 ± species, many of which are polytypic. Four families are restricted to insular habitats for breeding purposes.

Early ornithological field workers in Baja California concerned themselves with assembling specimen collections from one end of the peninsula to the other with little attention to the over-all avifaunal picture. The first attempt toward a comprehensive evaluation, slight as it was, came from Nelson (1921) in his monographic treatment of the natural resources of the peninsula. This was followed by Grinnell's (1928) well-known *Distributional summation of the ornithology of Lower California.*

Both of these pioneers of the subject stressed the importance of the Cape district, or terminal third of the peninsula, as an area rich in endemic species and subspecies of birds. Nelson defined the district as that portion of Baja California lying south of a line arching sharply to the north from Santa Rosalia on the Gulf coast to Punta Santo Domingo on the Pacific coast at Latitude 26° 19′ North. Grinnell (1928: 5), in his evaluation of the bird life of the peninsula, listed 46 species and subspecies of birds endemic to this region. Of these, he considered 43 to have arrived "from the north—over continuous land—rather than from the Gulf to the eastward (1928: 7)." Grinnell felt that the invasions of the Cape district probably occurred "by way of its basal territory, from California, Arizona and Sonora." This hypothesis of northern (in contrast to trans-gulf) origin of most of the vertebrates endemic to the Cape district was also held by Nelson. Grinnell (1928: 12) concluded that of all the areas of differentiation in Baja California, "it can be said that the Cape district appears to have acted most potently with respect to bird life." Thus Grinnell implied the idea that, in the Cape district, there has been a marked differentiation of pioneer ancestral stocks, and that because of this differentiation, the avifauna of that region now includes an unusually large number of endemic forms. Grinnell divided the peninsula into a number of differentiation centers in order of importance (1928: 5–7, also Fig. 1).

As early as 1919, Oberholser had shown that the brown towhee of the Cape district (*Pipilo fuscus albigula*), a form connected by a series of intergrading populations with the brown towhees of the Pacific coast of California, actually resembles *Pipilo fuscus mesoleucus* of Arizona, New Mexico, and northwestern Mexico more than it does the coastal races of California, in spite of the fact that *mesoleucus* on the one hand, and the brown towhees of California and Baja California on the other, are geographically

isolated. Davis (1951), in his excellent revision of the brown towhees, suggests that *albigula*, rather than being a strongly differentiated endemic of the Cape district, is actually a *non-differentiate*—a form that, far from being distinct from the ancestral stock that pioneered in the Cape district, might actually be similar to it. According to Davis's viewpoint, it is the brown towhees of the Pacific coast that have diverged farthest from the ancestral stock, leaving the towhee of the Cape district a relatively little differentiated relict contrasting sharply with them.

In a more recent paper, Davis (1959) endeavors to evaluate the variational trends exhibited by the endemic species and subspecies of birds that occur, at least in part, in the mountains of the Cape district, in order to test the "strong differentiate" versus "weak differentiate" hypothesis for this avifauna.

When Grinnell in 1928 pondered the question of endemism in the Cape district, he naturally could not draw upon the wealth of knowledge which has accumulated since that time, not only from new ornithological findings, but from a better understanding of the botanical relationships of the peninsula of Baja California with those of the mainland. Axelrod (1958) in his revealing work in this field has given the students of Baja California ornithology a valuable tool.

According to Axelrod (1958), the mountains of the Cape district support a vegetation that contains a Sierra Madrean woodland element evidently derived from the Madro-Tertiary flora. Miocene floras of southern California contain fossil equivalents of modern woodland species of the Cape highlands, together with fossil equivalents of living species typical of the California flora and fossil equivalents of species now occurring in the Sierra Madrean woodland in the interior southwestern United States and adjacent Mexico. The presence in the Cape highlands of modern plant species of definite Madro-Tertiary affinities suggests that the Madro-Tertiary flora moved northwestward from northern Mexico in the Miocene and, after reaching the Pacific coast, spread down the entire peninsula of Baja California and was replaced subsequently over most of the terminal two-thirds of the peninsula by the very rich desert flora found there today; the Sierra Madrean woodland element of the Madro-Tertiary flora persisted only in northwestern Baja California and in the highlands of the Cape district. This element, once widespread, probably provided the avenue of dispersal for acorn woodpeckers, robins, white-breasted nuthatches and the other upland species found in the Cape highlands today. In many instances these species are isolated from the nearest population of the same species or genus by a great expanse of unfavorable desert habitat. Since the Madro-Tertiary flora presumably originated in northern Mexico, it seems likely that the avian species associated today with the remnants of the Sierra Madrean woodland element in the Cape district actually followed this flora from northern Mexico to the Pacific coast and thence south down the length of the peninsula to the Cape. Various authors have stressed the probability that most of the vertebrate fauna in Baja California came from the north rather than across the Gulf of California. The birds presently associated with the Sierra Madrean woodland element seem especially favorable for consideration in this regard, as there is some evidence that suggests that these birds not only came from "the north," but more specifically from northern Mexico. The history of the Madro-Tertiary flora and the apparent correlation between the past movements of this flora and the present distribution of the brown towhee, as worked out by Davis, exemplifies the kind of population movements presumed typical for most of the species of birds found in the Cape highlands today.

Davis (1959) in his recent paper on the birds of the Cape highlands has selected

the endemics listed by Grinnell (1928) as occurring at least in part in the Laguna and Victoria mountains, and has subjected them to analysis with the following results:

(1) *Species with Mexican mainland affinities*

Of the 17 species and subspecies considered by Davis, 11 appear to have their closest relationships with related forms in Mexico and the southwestern United States, east of the Colorado River, rather than with the related forms on the Pacific coast of California. These 11 are as follows:

Columba fasciata vioscae—band-tailed pigeon
Otus asio xantusi—screech owl
Hylocharis xantusii—Xantus hummingbird
Melanerpes formicivorus angustifrons—acorn woodpecker
Sitta carolinensis lagunae—white-breasted nuthatch
Vireo huttoni cognatus—Hutton vireo
Vireo gilvus victorae—warbling vireo
Pipilo erythrophthalmus magnirostris—rufous-sided towhee
Pipilo fuscus albigula—brown towhee
Aimophila ruficeps sororia—rufous-crowned sparrow
Junco bairdi—Baird junco

(2) *Species with Pacific coastal affinities*

This group includes three species which clearly have their affinities with related forms found today on the Pacific coast to the northwest. These are as follows:

Aphelocoma coerulescens hypoleuca—scrub jay
Psaltriparus minimus grindae—common bushtit
Vireo solitarius lucasanus—solitary vireo

(3) *Strong Differentiates of the Cape district*

This last group includes three endemic forms which cannot be said to have particularly close affinities with other populations either to the northwest, northeast, or east. These are as follows:

Glaucidium gnoma hoskinsii—pygmy owl
Contopus sordidulus peninsulae—wood pewee
Turdus migratorius confinis—robin

This analysis made by Davis suggests strongly that most of the highland endemics of the Cape district colonized that region from the mainland of Mexico and the adjacent inland United States. Taking into consideration the habits of the species analyzed, it does not seem likely that such sedentary forms as the rufous-crowned sparrows, brown towhees, rufous-sided towhees, acorn woodpeckers and others would have invaded the Cape region by an overwater route, or even an island-hopping route from the Mexican mainland. It seems more likely that these species reached the Cape by either a direct land connection from the mainland or an overland route from northern Mexico through the adjacent southwestern United States to the base of the peninsula and then on down to the Cape region.

Anderson (1950) presented geologic evidence suggesting that the Gulf of California and the Peninsula of Baja California were blocked out in essentially their present form by early Pliocene. Colonization of the Cape region directly from the east by a land connection would, therefore, have had to occur by late Miocene at the latest. Such an invasion is improbable in view of the fact that only two of the 46 endemics of the Cape region listed by Grinnell can be thought of as being of west coast Mexican tropical origin. These two species are the groove-billed ani (*Crotophaga sulcirostris pallidula*), which also breeds in southern Sonora and may not be a Cape endemic at all, and the mangrove warbler (*Dendroica petechia castaneiceps*). Had invasion of the Cape occurred via a land connection from the east, it would be reasonable to expect the occurrence of a greater number of Mexican west coast

tropical species in the Cape region today, as, according to Axelrod, suitable habitat for such species existed as a border element to the Lagunan woodland by Miocene time. Arid tropical scrub genera such as *Acacia, Bursera, Dodonaea, Ficus* and *Lysiloma* are known to occur regularly with fossil representatives of the Lagunan woodland in the Miocene and Pliocene floras of southern California, and a number of these genera are prominent components of the lowland vegetation of the west coast of Mexico today from Sonora and Sinaloa southwards.

From the northwest, there intrudes a series of populations in northwestern Baja California (Davis's second group); these populations are evidently related to forms found on the Pacific coast of California. This suggests that the pioneering populations which had invaded the Pacific coast began to diverge morphologically, probably as the generalized Madro-Tertiary flora in the Pacific coastal region became segregated into modern communities such as pine-oak woodland, chaparral, and desert scrub. Axelrod has shown that in the Cape region, at least, the Sierra Madrean woodland element of the Madro-Tertiary flora has retained many of its original features. Such modern representatives of the Sierra Madrean woodland in the Cape region as *Arbutus peninsularis* and *Populus brandegeei* are represented by fossil equivalents in the Miocene of California and Nevada. Certain species found in the Cape highlands at the present time, including *Ilex brandegeana, Quercus albocincta,* and *Rhus hartmannii,* are known elsewhere only from the Sierra Madre Occidental in Sonora and Sinaloa.

Davis concludes (1959: 83) that, in assessing the "potency" with which the Cape district has acted on the birds of the highlands, it can be said that the Cape region has acted "potently" if the nature of the morphological variation in the endemics of the area is ignored. That is, if we are concerned merely with the number of recognizably distinct forms found in the Cape district, then it must be admitted that the region has been a particularly effective "center of differentiation." In opposition to this idea, the resemblance of most of the endemics of the Cape highlands to representatives of the same, or closely related, species in the interior southwestern United States and northern Mexico (from where the stocks ancestral to the endemics of the Cape region presumably came) suggests that in certain features the birds of the Cape highlands have diverged less from these ancestral stocks than have the representatives of these same species on the Pacific coast. If this viewpoint is accepted, the Cape region has not acted "potently" but, on the contrary, constitutes a center of relatively weak differentiation presumably because the habitat associated with the stocks pioneering into the Cape region has been relatively little altered in the Cape highlands, whereas it has become much more altered on the Pacific coast.

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Evolution of a Peninsular Herpetofauna

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BIOGEOGRAPHY is a field of theoretical biology that functions to formulate theories best explaining the current facts of distribution in the light of knowledge on physiography, climate, ecologic relations, geologic history, and evolution. Biogeographic theory is tested by new information or new interpretations of previously known data from all germane fields as these amplify, verify, or modify the theory as originally presented. The development of sound biogeographic theories depends upon:

1. Comprehensive analysis of present distributional patterns for each species in the area under consideration.
2. Knowledge of the basic ecologic associations and limits for each species.
3. Evaluation of the degrees of similarity and difference between the biota under study and those of other regions.
4. Correlation of known facts of geodynamic and paleoecologic history for the investigated area with present distributional patterns and ecologic and biogeographic relations. Application of these steps incorporates most of the advantages of both ecological and historical biogeography. In addition this approach produces a solid foundation in biogeographic statics (see Darlington, 1957, for a book concerned primarily with static zoogeography). The method is most significant, however, in providing a basis for discussion of the dynamics of the origin and evolution of biotas in terms of past physiographic, ecologic and biologic history, even in the absence of adequate fossil records.

The present paper forms an attempt to construct a cogent theory satisfactorily explaining the current distribution of the amphibians and reptiles of Baja California and the probable historical processes responsible for evolution of the peninsular herpetofauna. The attempt depends upon proper utilization of the method outlined above and previously employed in a study of the herpetofauna of central and southern California by Peabody and Savage (1958).

Baja California offers particularly intriguing ground for biogeographic investigations. With the exception of the Malay Peninsula, which extends approximately 1,000 miles from north to south, the 800 mile long peninsula of Baja California forms the longest, well-isolated peninsular area in the world. The peninsula is further unique in its long geologic existence as a discrete unit, dating back to Eocene (Durham and Allison, 1960). The vegetation of the area is well-known and indicates a wide diversity in climate and habitat, ranging from pine woodland, oak woodland, and chaparral in the north, through desert scrub to subtropical thorn-scrub in the south. In addition isolated southern ranges are covered by oak-pine woodlands and chaparral separated from northern communities of a similar nature by 300 miles of desert (Wiggins, 1960). The herpetofauna is comprised of four species of salamanders, eight frogs and toads, two kinds of nonmarine turtles, 39 lizards, and 35 species of snakes, a total of 88 forms. By comparison the climate and vegetation of the Malay Peninsula are relatively constant

over its entire extent and the herpetofauna is composed of approximately two species of caecilians, 80 frogs and toads, 20 turtles, 95 species of lizards, 115 snakes, three crocodilians and no salamanders, a total of 315 species. In addition to the Baja California Peninsula, numerous continental islands along the Pacific Coast and particularly adjacent to the peninsular mainland in the Gulf of California, support large faunas of reptiles and a few amphibians. In most cases a considerable amount of endemism is typical of each island. Although the distribution and origin of these insular faunas offer a fascinating project in biogeographic analysis, the problem is but a minor theme related to the larger problem of the evolution of the herpetofauna of the peninsula. For this reason insular species have not been considered in the general discussion in this paper, except in cases where insular forms provide clues to a better understanding of the major peninsular patterns. For readers interested in the island herpetofauna reference may be made to Schmidt (1922), Van Denburgh (1922), and Cliff (1954).

Recent North American Herpetofaunas

The present distribution and biogeographic relations of the amphibians and reptiles of Baja California cannot be treated properly without an understanding of the general distributional patterns for the entire North American herpetofauna. For the last 10 years I have been accumulating data for a report on the origins and affinities of the amphibian and reptile fauna of America north of the Isthmus of Tehuantepec. The emphasis in the initial stages of the study was upon detailed analyses of the distribution of known recent species in the region. Evaluation of these basic data indicates that six major and two minor herpetofaunal units occur in North America. Of course each of these entities is of diverse origins historically, but at the present time each unit occupies a physiographic area of distinct ecology, so that the general distribution of herpetofaunas may be plotted on a map (Fig. 1). The boundaries marking the geographic limits of the several faunal areas are somewhat arbitrary and denote a zone of relatively rapid transition from one fauna to another. The boundaries as drawn were determined by outlining the geographic range of each species and selecting a zone where the majority of ranges ended as the point of faunal change. The complexity of interdigitation, altitudinal effects, climate, and physiology all insure a constant shifting of the boundary zone on a small scale. However, application of Ekman's Rule (1953): the faunal boundary may be drawn at the point of greatest faunal change, makes possible an adequate approximation of the extent of each faunal region.

The eight herpetofaunas of North America include:

1. *Neotropical Herpetofauna*—reaching the area under discussion in Mexico, along the Atlantic coastal plain and in the coastal and foothill regions of the Pacific slope; a rich fauna of tropical origins continuous with similar faunal groups of Middle and South America; Stuart (1950) points out that the Caribbean and Pacific assemblages of this fauna may be recognized as distinct.

2. *Boreal North America Herpetofauna*—a depauperate fauna of elements capable of withstanding extremely cold winters; a very few snakes and a few amphibians make up this fauna.

3. *Eastern Forest Herpetofauna*—a fauna characterized by many species of salamanders, frogs, and turtles, found in the conifer and hardwood forest belt of the northeast and central portions of the continent.

4. *Austroriparian Herpetofauna*—a warm temperate fauna rich in species composition, particularly frogs, turtles, and snakes, occurring along the Atlantic and Gulf Coastal Plains and up the Mississippi Valley.

FIG. 1. Distribution of Recent North American herpetofaunas.

5. *Rocky Mountain Herpetofauna*—a depauperate fauna adapted for life in the rugged Rocky Mountain region; similar to Boreal North American Herpetofauna in group composition and species number.

6. *Pacific Border Herpetofauna*—restricted to the temperate coastal forest of the Pacific Northwest and its interior relicts; salamanders and frogs are the most striking elements of the herpetofauna.

7. *Sierra Madrean Herpetofauna*—found in warm climates associated with foothill physiography in California, Baja California, Arizona, New Mexico, and Mexico; dominated by lizard and snake species.

8. *Desert and Plains Herpetofauna*—a wide-ranging unit found in arid and semiarid regions of the American highlands; lizards and snakes are conspicuous elements.

These eight faunal entities exhibit different degrees of relationship to one another and it is convenient to group them into a comprehensive system (Table 1). Subdivisions of some importance are denoted in the table although not indicated on the map. The classification utilized follows the usual arrangement of biogeographic regions (Darlington, 1957). Each subregion is recognized on the basis of having a peculiar combination of families and genera and in being the center of adaptive radiation for many species groups. Biogeographic provinces in the sense employed here are not equal to the much smaller ecologic units called biotic provinces by Dice (1943). As used in this paper a Biogeographic Province is an area occupied by a distinctive major fauna, which differs from adjacent major faunal units in species composition. A useful device in determining the status of certain faunal regions is provided by a measure of faunal difference, the Coefficient of Difference (C.D.). The Coefficient of Difference for any two compared faunal units is calculated from the formula C.D. $= 1 - \frac{C}{N_2} \times 100\%$. C is equal to the number of species common to the two areas and N_2 is equal to the number of species in the larger of the two faunas. It has been found in the course of my analysis that major faunal differences are indicated when the C.D. is equal to 50% or more. As a convenience herpetofaunal provinces in this system are faunal units having a C.D. equal to or greater than 50% when compared to any other fauna.

It will be noted that the herpetofauna of Baja California is composed of elements from two of the major recent herpetofaunas, the Sierra Madrean and Desert and Plains units.

TABLE 1—DISTRIBUTION OF NORTH AMERICAN HERPETOFAUNAS—RECENT

NEARCTIC REGION

- I. BOREAL NORTH AMERICAN SUBREGION
- II. EASTERN NORTH AMERICAN SUBREGION
  - A. Eastern Forest Province
    1. Northeastern American Subprovince
    2. Appalachian-Ozarkian Subprovince
  - B. Austroriparian Province
- III. WESTERN MONTANE SUBREGION
  - A. Rocky Mountain Province
    1. Northern Rocky Mountain Subprovince
    2. Southern Rocky Mountain Subprovince
  - B. Pacific Border Province
- IV. AMERICAN HIGHLAND SUBREGION
  - A. Sierra Madrean Province
    1. Californian Subprovince
    2. San Lucan Subprovince
    3. Arizonian Subprovince
    4. Sierra Madre Occidental Subprovince
    5. Sierra Madre del Sur Subprovince
    6. Sierra Madre Oriental Subprovince
  - B. Desert and Plains Province
    1. Great Plains Subprovince
    2. Chihuahua Desert Subprovince
    3. Sonoran Desert Subprovince

NEOTROPICAL REGION

Historical Elements of North American Herpetofaunas

Emmett Reid Dunn (1931) was the first to attempt an explanation of the centers of origin and evolution for the American herpetofaunas. His interpretations were based on analysis of modern distributional data, conservative geological principles, and general acceptance of the ideas of Matthew (1915) as these are applicable in terms of amphibian and reptile ecology. Dunn recognized three principal faunal units: a) The South American Element, b) The Old Northern Element, and c) The Holarctic Element. He regarded these units as derived from three historical waves, each sweeping down from the north into southern areas. The oldest wave according to Dunn was the South American Element which moved into Latin America during late Cretaceous and early Tertiary times. Dunn suggested that his Old Northern Element reached Middle America in Miocene and swept on into South America after the closure of the Panamanian portal in the Pliocene. The Holarctic Element was conceived of as a very modern circumpolar unit which crossed into North America from Asia in Pliocene and Pleistocene times. Stuart (1950, 1951, 1954a, 1954b, 1957, 1958) more recently has suggested a fourth major element, the Autochthonous Middle American Element, which developed from northern groups of the South American Element following the submergence of the Panamanian bridge in early Tertiary. Stuart's Autochthonous Middle American Element includes certain groups placed by Dunn in his South American Element.

Dunn and Stuart were both hampered to a considerable extent in their analyses by the lack of fossil herpetofaunas for Cenozoic times, particularly of the crucial middle Tertiary. This handicap is still a reality in any attempt to evaluate the history of the North American herpetofaunas, although recent finds or reworking of old materials (Brattstrom, 1955a, 1955b, 1958a, 1958b; Hecht, 1959; Zweifel, 1956) now give herpetologists some hints in developing theories of faunal origin. Unfortunately, the fossil finds for western North America (reviewed by Peabody and Savage, 1958) are relatively rare and currently no amphibians or reptiles of pre-Pleistocene age are known from Baja California. As a result evaluation of the broad panorama of herpetofaunal differentiation in North America and particularly in the critical areas of the west must be based upon correlations with documented physiographic and ecologic changes during Cenozoic.

A particularly valuable asset provided the biogeographer of Cenozoic times and not considered in the work of Dunn and Stuart is the extensive paleobotanic record for the Era gradually uncovered during the last 30 years. Of greatest significance to the present thesis is the concept of three major geofloras undergoing evolution and dispersion in the Americas during Tertiary times as developed by Chaney (1938, 1940, 1944, 1947) and Axelrod (1950). Elsewhere (Peabody and Savage, 1958) I have pointed out that the Cenozoic herpetofaunas of the west may be correlated broadly with these Tertiary geofloras. In fact I am now convinced that correlation of geologic and geofloral history forms a firm basis for revaluation and further development of concepts of the historical origins, relationships, and dispersion of the fundamental herpetofaunal elements found today throughout North America. The fundamental historical units of modern herpetofaunas and the distribution of the herpetofaunas themselves as outlined in the previous section exhibit a striking association with one or the other of the three Tertiary geofloras, and distinctive plant associations derived from these geofloras today dominate each of the biogeographic areas described above (Fig. 1, Table 1). That the association of herpetofaunas and geofloras is a long-term condition is indicated by the scanty fossil record. Brattstrom (1955a) finds essentially

tropical species in Eocene material from near San Diego associated with tropical vegetation now found far to the south. Hecht (1959) in considering a tropical or subtropical faunal unit from Wyoming Eocene deposits concludes that descendent forms are now found in Middle America and his material is from an area well represented by Eocene floral material of a tropical type, today found far to the south in Middle America. Peabody (1954, 1959) also presents evidence for the close association of herpetofaunas with geofloral aggregations through time. His material of a fossil ambystomatid from the Paleocene of Montana and of a salamander assemblage from the early Pliocene of the Sierra Nevada of California demonstrates clearly the continuous association of representatives of modern genera or their close allies with temperate forests similar to those still occupied by these forms.

The three Tertiary geofloras represented in North America and the modern herpetofaunas associated with their derivative elements are as follows:

Neotropical Tertiary Geoflora—Neotropical Herpetofauna.

Arcto-Tertiary Geoflora—Boreal North American, Eastern Forest, Austroriparian, Rocky Mountain, and Pacific Border Herpetofaunas.

Madro-Tertiary Geoflora—Sierra Madrean and Desert and Plains Herpetofaunas.

Naturally, a given herpetofauna is composed of a complement of species originating from several sources. A considerable proportion of the species in each unit, however, originated in or near the area now occupied by the faunal assemblage. For these reasons present day herpetofaunas are mixtures of species of diverse historical origins, although a particular fauna is dominated by derivatives of one of the historical units defined below. Since these historical elements of the modern herpetofaunas show a close correlation with the well-documented geofloras in both current and past distribution, the major features of herpetofaunal history may be perceived and followed through the obscuring mists of time by reference to the known facts of geofloral and ecologic history combined with an appreciation of geologic change. The fundamental historical assemblages, their geofloral associations, optimum climatic requirements, and their place and time of origin are summarized below and in tabular form (Table 2).

South American Element—descendents of the generalized Tropical American herpetofauna that dominated much of North and South America in early Tertiary; the South American Element originated from the Tropical American groups restricted during most of Cenozoic to the South American island, but subsequently invaded Middle America after closure of the Panamian portal in late Tertiary (Simpson, 1950); associated with the Neotropical Tertiary Geoflora; corresponds to South American Element of Stuart (1950).

Middle American Element—descendents of tropical groups trapped in Middle America by inundation of the Panamanian Isthmus in early Tertiary; derived *in situ* in Middle America from ancestors belonging to the generalized Tropical American herpetofauna; associated with the Neotropical Tertiary Geoflora; equal to the Autochthonous Middle American Element of Stuart (1950) who traces its history in Central America.

Old Northern Element—descendents of temperate circumpolar groups found in the far northern continental areas in early Tertiary, but forced southward as the limits of tropic and temperate zones were restricted during the long-term climatic shift throughout Tertiary time; origin in areas around the Arctic basin, but now found far to the south and eliminated from the extreme north; associated with the Arcto-Tertiary Geoflora; corresponds to older element of Old Northern Element of Dunn (1931).

TABLE 2—HISTORICAL ELEMENTS OF NORTH AMERICAN HERPETOFAUNAS

UNITS	GEOFLORAL ASSOCIATION	CLIMATE	ORIGIN	EXAMPLES
A. SOUTH AMERICAN ELEMENT	Neotropical Tertiary	Tropical	From generalized Tropical American unit; ultimately from Paleotropics	*Atelopus* *Atractus* *Caiman*
B. OLD NORTHERN ELEMENT	Arcto-Tertiary		Palearctic	
1. Eastern American Complex		Cool temperate		*Cryptobranchus* *Gyrinophilus*
2. Western American Complex		Cool temperate		*Dicamptodon* *Ascaphus*
3. Central American Complex		Warm temperate		*Pseudoeurycea* *Staurotypus*
4. Southeastern American Complex		Warm temperate		*Siren* *Graptemys*
C. MIDDLE AMERICAN ELEMENT	Neotropical Tertiary	Tropical, subtropical	From generalized Tropical American unit	*Basciliscus* *Xenosaurus*
D. YOUNG NORTHERN ELEMENT	Madro-Tertiary		From generalized Tropical American unit	
1. Madrean Complex		Subhumid		*Gerrhonotus*
2. Desert and Plains Complex		Semiarid, arid		*Crotaphytus* *Phyllorhynchus*
E. HOLARCTIC ELEMENT	Arcto-Tertiary	Cool temperate	Recent invaders from Eurasia	*Bufo boreas* *Rana sylvatica*

Arranged in approximate order from most ancient to most recent in America.

Young Northern Element—descendents of generalized Tropical American herpetofauna of early Tertiary isolated in North America by the Panamanian portal and subjugated to the stimulus of extreme physiographic revolution and the increasing climatic shift toward arid conditions characteristic of middle and late Cenozoic times in western North America, including Mexico; originating *in situ* from tropical ancestors beginning in mid-Eocene and becoming well-established if not dominant over vast areas of subhumid to arid climates and diverse topography by mid-Miocene; closely associated with the Madro-Tertiary Geoflora; equal to younger element of Old Northern Element of Dunn (1931).

Holarctic Element—modern circumpolar species groups closely allied to Eurasian types; probably recently derived from Eurasian forms in late Cenozoic and reaching America across the Bering land connection in Pliocene and Pleistocene (Simpson, 1947); associated with modern coniferous and deciduous forest components of the Arcto-Tertiary Geoflora; part of the Holarctic Element of Dunn (1931).

Contrary to the views of Dunn (1931) and Stuart (1950) the principal feature of herpetofaunal evolution in North America has been the *in situ* development of newer faunal elements from descendents of the faunas represented early in Tertiary time, rather than through waves of north-south dispersion. Basically, the Americas in early Cenozoic were occupied by two principal faunal groups: a) in the north by the ancestral Old Northern genera associated with the Arcto-Tertiary Geoflora in what is now the extreme northern United States north to the Arctic Sea; and b) over the rest of the American continents by the generalized Tropical American herpetofauna associated with the Neotropical Tertiary Geoflora. After separation of the two continents in late Paleocene the ancestral Tropical American herpetofauna underwent evolution in three primary centers: 1) in isolation in South America to become the basic herpetofauna of the region today; 2) in the area just north of the Panamanian portal from stranded groups rather closely allied to their South American cognates; and 3) in the western United States and Mexico. The first mentioned forms evolved into the South American Element associated with Neotropical Tertiary vegetation. The second group developed into the Middle American Element which is also associated with Neotropical Tertiary vegetation. The third element, the Young Northern Element, did not become fully differentiated until middle Cenozoic following the rapid physiographic and climatic changes affecting western North America from Eocene onward. Concurrent with the origin of the Young Northern Element in response to the changing environments of Middle Tertiary times, the Old Northern Element expanded southward as a general trend toward lower temperatures affected the region. The climatic shift ultimately restricted the Neotropical Tertiary geofloral derivatives to their present area of tropical occurrence. In the western and central portions of North America a long-term tendency toward increasing aridity produced a new vegetational association, the Madro-Tertiary Geoflora, from marginal Neotropical Tertiary types. Evolving in association with the Madro-Tertiary Geoflora from Oligocene onward has been the Young Northern Element of the herpetofauna, likewise derived from generalized Tropical American ancestors but gradually becoming adapted to arid conditions. Members of the Holarctic Element invaded the continent across the Bering land corridor at the time of Pliocene and early Pleistocene emergence and constitute a very small part of the total species composition of the modern American herpetofauna.

In summary, early Tertiary herpetofaunal elements were two in number, a generalized Tropical American unit and a temperate unit ancestral to the Old Northern Element. Physiographic and climatic changes provided the necessary circumstances and stimulus to the development

of South American and Middle American Elements from the Tropical American unit in the tropics and of an arid derivative of the Tropical American unit in the warmer temperate regions, the Young Northern Element. The Old Northern Element of cooler and more humid areas has moved southward as the result of long-term cooling trends through Cenozoic, but has not successfully invaded the areas of Young Northern dominance because of the semiarid or arid environment. Representatives of the Holarctic Element of the cool temperate type have recently invaded the northern area of the continent. As shown by Axelrod (1958), Durham (1950), King (1958), MacGinitie (1958), and Simpson (1947, 1950) these views are fully compatible with current understanding of the physiographic, geologic, paleobotanic, and ecologic history of North America.

In detailed studies of herpetofaunistics it is usually necessary to evaluate historical origin more fully than is possible when only the five major elements are considered. Subdivision of each of the elements into units representative of the centers of differentiation within them increases the usefulness of the system. Species groups from primary centers of origin and dispersion of each element may be referred to as *complexes*. Minor units within a complex are called *components*. The herpetofaunal complexes of importance to an understanding of the development of the herpetofauna of Baja California are indicated in the accompanying table (Table 2). Inasmuch as the peninsula is dominated by species typical of the Desert and Plains and Madrean Complexes, the components of these two complexes are outlined in tabular form (Table 3). Current distribution of the majority of species within a given complex or component centers around appropriate biogeographic province or subprovince limits, respectively. However, no herpetofaunal province or subprovince is populated exclusively by a single historical complex. Utilization of the complex and component concepts are extremely useful in evaluating the historical relationships of any assemblage of amphibians and reptiles. They may be employed in evaluation of the faunal composition for recent faunas, as will be undertaken in the next section of this paper, or in determination of the relationships of fossil assemblages. Component analysis for fossil faunas is particularly important in ascertaining the previous distribution and possible history of the particular species assemblage under investigation.

TABLE 3—COMPONENTS OF AMERICAN HIGHLAND FAUNA

MADREAN COMPLEX

- Californian Component—oak woodland, chaparral, pine woodland
- Arizonian Component—oak woodland, chaparral, pine woodland
- San Lucan Component—thorn-scrub, oak woodland, chaparral, pine woodland
- Sierra Madre Occidental Component—oak-pine woodland, chaparral
- Sierra Madre del Sur Component—oak-pine woodland
- Sierra Madre Oriental Component—oak-pine woodland, chaparral

DESERT AND PLAINS COMPLEX

- Great Plains Component—grasslands
- Chihuahua Desert Component—desert woodland and scrub
- Sonoran Desert Component—desert woodland and scrub

Actual application of this method to a particular fossil fauna may prove enlightening. Etheridge (1958) has recently discussed the herpetofauna of a Pleistocene locality from Cragin Quarry, Meade County, Kansas. This fauna is composed of remains of six species of lizards. Analysis of the small assemblage indicates that the members may be divided by complex or component as follows: 50% Chihuahua Desert Component, 40% Great Plains Component, and 10% Southeastern American Complex. These data indicate that forms now making up the Chihuahua Desert herpetofauna sometime in Pleistocene occurred farther north than at present and that the Cragin Quarry fauna may

have lived in an area of mixed desert and grassland conditions.

In conclusion it must be emphasized that the basic unit of evaluation in utilizing the historical elements defined above is not the family or genus (contrary to Dunn, 1931). Species and species groups may be typical of a particular element, while other members of the same genus may have evolved as part of some other element. The genus *Rana* is an excellent case in point. Very clearly certain members of the group have entered America only recently and are part of the circumpolar Holarctic Element (*Rana aurora, Rana pretiosa,* and *Rana sylvatica,* for example). Other groups, as an example *Rana boylii* and its allies, have evolved as members of the Young Northern Element in conjunction with the development of Madro-Tertiary vegetation. Still other species groups, for example *Rana catesbeiana* and relatives, appear to be part of the very ancient Old Northern Element. In all likelihood the genus *Rana* has been in North America throughout most of Cenozoic and reference of the entire genus to one or the other historical element is misleading.

The Herpetofauna of Baja California

As pointed out in previous sections the recent herpetofauna of Baja California belongs to either the Sierra Madrean or Desert and Plains Provinces of the American Highland Subregion. The majority of species are representatives of the Young Northern Element, but some forms from the Old Northern Element are also present. The distribution of the recent species may be summarized as follows (see Fig. 2, Table 4):

1. A northwestern assemblage continuous with the herpetofauna of coastal and montane Alta California and associated with coastal sage scrub, oak woodland, chaparral, and pine woodland communities in a winter rain climatic area—The Californian Subprovince.

2. A northeastern desert assemblage continuous with the Colorado, Mojave, Arizona, and Sonora Desert areas and dominated by desert woodland and scrub vegetation in very arid winter rain belt—The Colorado Desert District.

3. A central peninsular assemblage occurring to the south of the California and Colorado Desert areas, also covered by desert woodland and scrub vegetation in an arid summer rain belt—The Peninsular Desert District.

4. An assemblage in the Cape region and montane areas to the north found east and south of the Peninsular Desert groups, associated with subtropical thornscrub, oak woodland, chaparral, and pine woodland communities in a summer rain climate—The San Lucan Subprovince.

The Californian and San Lucan Subprovinces are portions of the Sierra Madrean Province. The Colorado and Peninsular Desert Districts are subdivisions of the Sonoran Desert Subprovince of the Desert and Plains Province.

The general distribution of each species in the herpetofauna by basic areas is presented in the accompanying table (Table 4). Comparisons based upon the limits indicated for the biotic areas above and outlined on the accompanying map (Fig. 2) among these four units are presented in tabular form (Table 5). Interpretation of the faunal analysis is relatively simple. The Californian, San Lucan, and Colorado Desert centers differ markedly from one another, although a considerable degree of relationship is suggested for the first two. The Peninsular Desert area on the other hand is poorly differentiated from both the Colorado Desert and San Lucan faunas. As a matter of fact it seems to represent a transitional belt between the two, although different from both in total faunal aggregation. Another way in which to verify this concept is provided in an analysis of the degrees of endemism in each faunal unit (Table 6A). Again the Californian, San Lucan, and Colorado Desert areas are distinctive but not a single endemic occurs

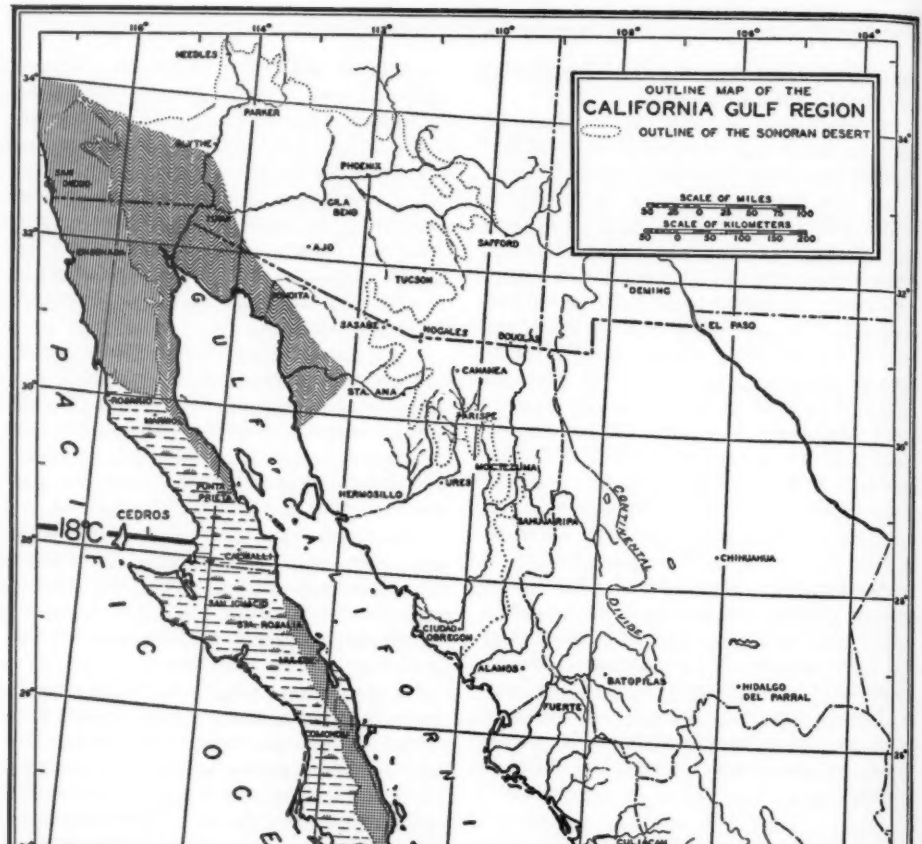

FIG. 2. Herpetofaunal areas of Baja California. Note the location of the minimum winter isotherms for marine surface temperatures.

TABLE 4—DISTRIBUTION OF THE BAJA CALIFORNIA HERPETOFAUNA BY FAUNAL AREA

SPECIES	CALIFORNIAN	COLORADO DESERT	PENINSULAR DESERT	SAN LUCAN
SALAMANDERS:				
Aneides lugubris	C			
Batrachoseps sp.	C			
Batrachoseps pacificus	C			
Ensatina eschscholtzii	C			
FROGS AND TOADS:				
Scaphiopus couchii			X	X
Scaphiopus hammondii	C			
Bufo boreas	C			
Bufo microscaphus	C			
Bufo punctatus	X	X	X	X
Hyla arenicolor	C			
Hyla regilla	X			X
Rana aurora	C			
TURTLES:				
Clemmys marmorata	C			
Pseudemys scripta				X
LIZARDS:				
Coleonyx variegatus	X	X	X	X
Phyllodactylus unctus				E
Phyllodactylus xanti		X	X	X
Xantusia henshawi	C			
Xantusia vigilis		X	X	X
Callisaurus draconoides		X	X	X
Crotaphytus collaris		X	X	
Ctenosaura hemilopha				C
Dipsosaurus dorsalis		X	X	X
Gambelia wislizenii		X	X	X
Phrynosoma coronatum	X		X	X
Phrynosoma m'callii		C		
Phrynosoma platyrhinos		C		
Sauromalus australis			X	X
Sauromalus obesus		C		
Sceloporus graciosus	C			
Sceloporus magister	X	X	X	X
Sceloporus occidentalis	C			
Sceloporus orcutti	X		X	X
Uma notata		C		
Urosaurus graciosus		C		
Urosaurus microscutatus		X	X	
Urosaurus nigricaudus				X
Urosaurus ornatus		C		
Uta mearnsi		C		
Uta stansburiana	X	X	X	X
Uta thalassina				E
Eumeces gilberti	C			
Eumeces lagunensis				E
Eumeces skiltonianus	C			
Cnemidophorus hyperythrus	X		X	X
Cnemidophorus labialis	E			
Cnemidophorus maximus				E
Cnemidophorus tigris	X	X	X	X
Bipes biporus			X	X
Gerrhonotus multicarinatus	C			
Gerrhonotus paucicarinatus				E
Anniella geronimensis	E			
Anniella pulchra	C			

TABLE 4—Continued

SPECIES	CALIFORNIAN	COLORADO DESERT	PENINSULAR DESERT	SAN LUCAN
SNAKES:				
Leptotyphlops humilis	X	X	X	X
Lichanura trivirgata	X			X
Arizona elegans	X	X	X	
Chilomeniscus cinctus	X		X	
Chilomeniscus stramineus				E
Coluber aurigulus				E
Coluber flagellum	X	X	X	X
Coluber lateralis	X		X	
Diadophis amabilis	C			
Elaphae rosaliae				E
Hypsiglena torquata	X	X	X	X
Eridiphas slevini				E
Lampropeltis getulus	X			X
Lampropletis zonata	C			
Natrix valida				C
Pituophis melanoleucus	X	X	X	X
Phyllorhynchus decurtatus		X	X	X
Rhinocheilus lecontei	X	X		
Salvadora hexalepis	X	X	X	X
Sonora bancroftae	E			
Sonora mosaueri			X	X
Sonora semianulata		C		
Tantilla eiseni	C			
Tantilla planiceps				E
Thamnophis couchii	C			
Thamnophis digueti				E
Thamnophis elegans	C			E
Trimorphodon lyrophanes				
Trimorphodon vandenburghi	C			
Crotalus atrox		C		
Crotalus cerastes		C		
Crotalus enyo	X		X	X
Crotalus mitchellii	X	X	X	X
Crotalus ruber	X	X	X	X
Crotalus viridis	X		X	
TOTALS:	50	32	32	45

X = present; E = endemic; C = endemic to area in Baja California but found elsewhere. Because of the complexities of transitional areas, certain species that barely penetrate the margins of a particular faunal area have not been included.

in the Peninsular Desert. All species in this zone are found elsewhere on the peninsula, suggesting that the Peninsular Desert has been invaded by forms from the north and south. In another table (Table 6B) the actual composition of the Peninsular Desert herpetofauna and its probable sources are indicated.

Further analysis of distribution patterns provides a detailed picture of 13 different basic distributions with reference to the faunal areas. All 88 species of Baja California amphibians and reptiles fall into one of these patterns as indicated by percentages of the total faunal composition. Characteristic distributional patterns are illustrated in range maps (Figs. 3–7).

The relations of the total herpetofauna of the Peninsula to the rest of North America are surveyed in tabular form (Table 7) to complete the analysis. The table is designed to evaluate the general composition of the Baja California assemblage in terms of the historical complexes discussed in a previous section.

TABLE 5—COMPARISONS BETWEEN FAUNAL AREAS OF BAJA CALIFORNIA

	COEFFICIENT OF DIFFERENCE (C.D.)
Californian—Colorado Desert	72%
Californian—Peninsular Desert	60%
Californian—San Lucan	62%
Colorado Desert—Peninsular Desert.	34%
Colorado Desert—San Lucan	60%
San Lucan—Peninsular Desert	41%

$$C.D. = 1 - \frac{C}{N_s} \times 100$$

C = elements in common

N_s = total number of elements in larger fauna

The dominant forms in the region are members of the Young Northern Element. However, a significant but small representation of the species from the Pacific Border Component of the Western American Complex (Old Northern Element) is also present. All of the species from this latter assemblage are restricted to the Californian faunal area of relatively high winter rainfall and cool temperatures.

Origins and History of Baja California Herpetofauna

The composition and distribution of the amphibian and reptile fauna of Baja California are the products of complex interactions between a changing Cenozoic environment and the ancestral stocks of living species. The essential features of the history of the peninsular herpetofauna are variations on a theme of physiographic and climatic revolution throughout western North America from mid-Eocene to the present, with local emphasis provided by the barrier to dispersion formed by the Gulf of California. The detailed distribution of modern species within the region are the results of Pleistocene events but the dynamic evolution of the essential ingredients of the Baja California herpetofauna was initiated much earlier in Tertiary times.

The peninsula has existed as a more or less stable physiographic unit since the Eocene, with considerable fluctuation in southern extent between Eocene and Pliocene (Beal, 1948; Durham and Allison, 1960). The Gulf of California has acted as a strong barrier to biotic dispersion between the Mexican mainland and Baja California throughout peninsular history. The Gulf barrier was further intensified during most of Cenozoic since the marine waters reached northward into the Coachella Valley area of southern California to a much greater extent than at present. The stability of the peninsula and the long-term existence of a salt-water barrier to the east have required that all terrestrial immigrants, with the possible exception of a few trans-Gulf invaders,

TABLE 6—LEVELS OF DISTINCTIVENESS IN BAJA CALIFORNIA HERPETOFAUNAS

A. DEGREES OF ENDEMISM

FAUNAL AREA	N = TOTAL NO. SPECIES	E = ENDEMIC SPECIES	E/N × 100%
Californian	50	26	52%
Colorado Desert	32	10	31%
Peninsular Desert	32	0	0%
San Lucan	45	16	35%

B. COMPOSITION OF PENINSULAR DESERT FAUNA

FAUNAL UNIT	1.	2.
Californian	62%	25%
Colorado Desert	66%	28%
San Lucan	81%	44%

1. = % of total Peninsular Desert fauna found in other areas.
2. = % of total Peninsular Desert fauna found in other areas, exclusive of ubiquitous species.

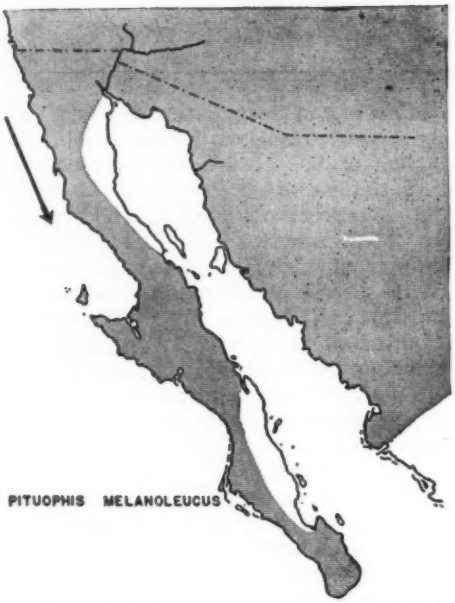

FIG. 3. Range of gopher snake, *Pituophis melanoleucus*, a ubiquitous Baja California species. Solid arrow indicates direction of dispersal since most recent glacial period.

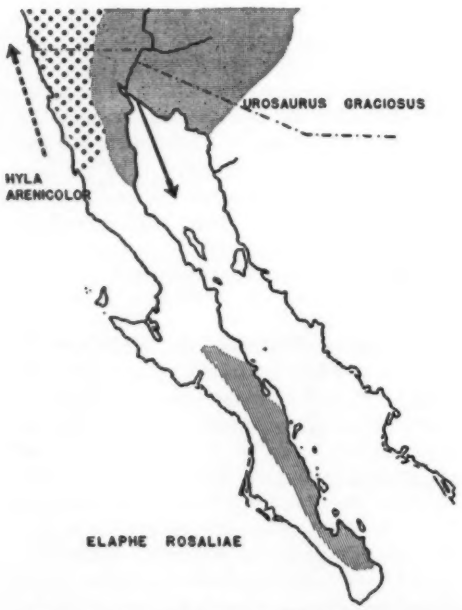

FIG. 4. Ranges of a Californian area endemic, cañon tree-toad, *Hyla arenicolor;* a Colorado Desert endemic, long-tailed bush lizard, *Urosaurus graciosus;* and a San Lucan endemic, Baja California ratsnake, *Elaphe rosaliae*. Solid arrow indicates direction of dispersion since most recent glacial recession; dashed arrow direction of contraction of range.

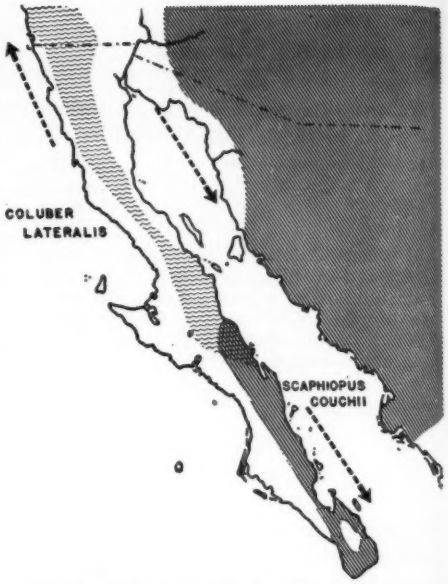

FIG. 5. Ranges of species occurring in two faunal areas in Baja California: a species with a Californian-Peninsular Desert distribution, California striped whipsnake, *Coluber lateralis;* a form with a Peninsular Desert-San Lucan distribution, Great Plains spadefoot, *Scaphiopus couchii*. Dashed arrows indicate direction of contraction of range with increasing aridity.

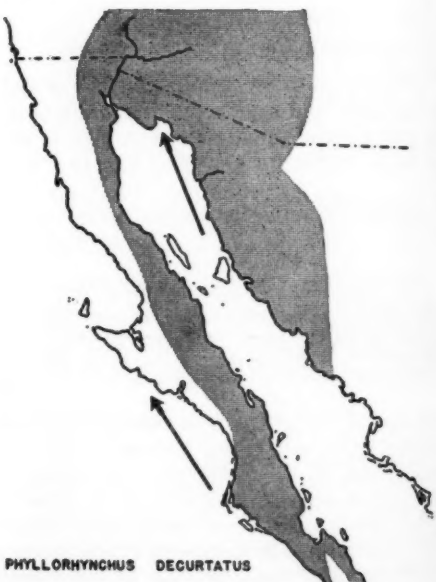

FIG. 6. Example of species occurring in three of the four major biotic areas of Baja California: the leaf-nosed snake, *Phyllorhynchus decurtatus*. Solid arrow indicates direction of dispersal into areas on increasing aridity since latest glacial recession.

FIG. 7. Example of distribution pattern of paired allopatric species found in Californian and San Lucan biotic areas: the California alligator lizard, *Gerrhonotus multicarinatus*, and the San Lucan alligator lizard, *Gerrhonotus paucicarinatus*. Note the occurrence of a third allopatric form, *Gerrhonotus cedrosensis*, on Cedros Island off the Pacific coast of the peninsula. Broken arrows indicate contraction of ranges since glacial maximum.

1. Ubiquitous (found in all four areas)	13%
2. Endemic (total)	57%
Californian	28%
Colorado Desert	11%
San Lucan	18%
3. Restricted to Two Areas (total)	14%
Californian—Colorado Desert	1%
Californian—Peninsular Desert	3%
Californian—San Lucan	3%
Colorado Desert—Peninsular Desert	2%
Peninsular Desert—San Lucan	5%
4. Absent from One Area (total)	11%
Californian	5%
Colorado Desert	4%
San Lucan	1%
5. Paired Allopatric Species (Californian-San Lucan)	6%

enter the region from the north. The present herpetofaunal assemblage of Baja California consists primarily of northern migrants or western Mexican forms that have invaded the peninsula from the north after passing around the head of the Gulf of California.

TABLE 7—RELATIONSHIPS OF TOTAL BAJA CALIFORNIA FAUNA (88 SPECIES)

FAUNAS	% OF COMMON SPECIES
1. Eastern Forest Complex	2
2. Southeastern Coastal Plains Complex	3
3. Western American Complex	
a. Rocky Mountain Component	9
b. Pacific Border Component	18
4. Madrean Complex	
a. Californian Component	51
b. Arizonian Component	14
c. Sierra Madre Occidental Component	9
d. Sierra Madre del Sur Component	3
e. Sierra Madre Oriental Component	5
f. San Lucan Component	50
5. Desert and Plains Complex	
a. Sonoran Desert Component	50
b. Chihuahua Desert Component	24
c. Great Plains Component	21
6. Middle American Element	3

The geologic history of Baja California is closely associated with the development of the rest of western North America. As brilliantly outlined by King (1958) the entire western continental region has undergone vast physiographic convulsions and radical change from Eocene to the present. Of greatest significance to the evolution of current distribution patterns was extensive mountain building activity in late Cenozoic. Generally important to the development of the distinctive western herpetofauna was the uplift of the Rocky Mountain cordillera of the central United States and Mexico from Eocene onward as these ranges came to isolate the western regions from the influences of eastern groups. Of principal importance to evolution in Baja California was the uplift of the Sierra Nevada and Peninsular Ranges of the Pacific region to their present great heights during late Pliocene and Pleistocene. The effects of

mountain building were most pronounced in northern Baja California where the Sierra Juarez and Sierra San Pedro Mártir attained maximum elevation to 10,000 feet and in the Cape region where the Sierra Laguna and Sierra Victoria attained elevations of 6,200 feet. Vulcanism contributed to the formation of mountains in the central peninsula in late Miocene, and some individual peaks of these ranges reach altitudes over 6,000 feet at the present. Mountain building contributed in two important ways to the development of the modern herpetofauna by 1) providing areas where altitudinal ecologic effects allowed the entrance into the peninsula of forms typical of cooler and moister areas to the north, and 2) making possible dispersion along ecologically suitable foothill environments southward into the Cape region during periods of lower temperature and higher rainfall in Pleistocene. Another minor effect, in the north, was the contribution to rain-shadow as relating to the development of arid conditions in the Colorado Desert. The central and cape mountain ranges may have also had a rain-shadow effect on the lowlands of adjacent western Mexico in the Pleistocene when the major storm-tracks must have moved across the peninsula toward Mexico. Today the principal storms moving into the area of the Mexican lowlands opposite the peninsula move up the Gulf of California from south to north and the peninsular ranges have little effect on rainfall characteristics of the adjacent mainland.

Climatic conditions and the general ecology of the peninsula have undergone marked changes since mid-Eocene correlated in a broad sense with the geologic and physiographic shifts summarized above. Although no well-documented fossil record of the terrestrial life of Baja California exists, the data from marine fossils and knowledge of the paleobotanic record elsewhere in western America allow reconstructions of the basic paleoecology of the peninsula throughout Cenozoic. The generalized survey that follows is based upon an interpretation of the marine data discussed by Durham (1950, 1954), and Durham and Allison (1960), integrated with the concepts of terrestrial paleoecology and vegetational evolution developed by Chaney (1938, 1940, 1944, 1947) and Axelrod (1950), and summarized by Axelrod (1948, 1950, 1956, 1957, 1958) and MacGinitie (1958).

In early Tertiary times the region which is now Baja California was covered by a humid tropical forest characteristic of the Neotropical Tertiary Geoflora. Forest associations of this general type apparently ranged as far north as present day southern Canada (Axelrod, 1958). Generally similar climatic and vegetational conditions apparently persisted in the region until at least Eocene time.

In the Eocene, MacGinitie (1958) reports three principal floras from western North America: a) a subtropic forest extending along the coast to about 55° N. Latitude (near the level of the minimum February isotherm of 18° C., according to Durham, 1950, and inland at least to Wyoming); b) a tropical flora along the Mississippi embayment coast in what is now western Texas and central New Mexico; and c) far to the north the warm temperate Arcto-Tertiary forests. Baja California appears to have been occupied by subtropical and possibly tropical forests at this period. Marine surface temperatures (winter minimum) were over 25° C. at the latitude of Cabo San Lucas.

During Oligocene there seems to have been a shift toward cooler temperatures along the western coasts (the 18° C., minimum isotherm for February was near 50° N. Latitude) and reduction in rainfall. However, no major changes in vegetation occurred until Miocene when elements of the Madro-Tertiary Geoflora appear to take on a greater dominance in response to a general increase in aridity (Axelrod, 1958). However, even in early Miocene the vegetation and climate of Baja California were probably similar to those of the adjacent Mexican mainland with subtropical vegetation predominating. By

late Miocene subtropical environments were probably restricted southward or to the coastal areas by cooling temperatures and increasing aridity. The winter minimum isotherm of 18° C., was at the latitude of Los Angeles and the 25° isotherm was at the level of Cabo San Lucas by this time. Madro-Tertiary elements, particularly thorn-scrub, probably dominated over much of the northern two-thirds of the peninsula.

In the Pliocene the combined effects of temperature decrease, increased aridity, and mountain building activity appear to have resulted in restriction of the thorn-scrub to extreme southern Baja California. A continuous Madro-Tertiary floral unit of mixed oak woodland, chaparral, and more arid forms expanded down the length of the peninsula, and desert elements began to appear in the rain-shadow area of the northeast. In addition Arcto-Tertiary floral components probably entered Baja California for the first time on the higher ridges of the developing Sierra of northern Baja California. By the end of the Pliocene the modern floral units found in Baja California seem to have been established. The thorn-scrub complex persisted in the Cape region lowlands of relatively high temperatures and rainfall. The oak woodland and chaparral communities of the Madro-Tertiary Geoflora dominated as a continuous floral belt from the north throughout the waist of the peninsula and into the uplands of the Cape region. Desert vegetation probably was developing rapidly in areas of low rainfall in the northeast and gulf coastal areas under the influence of rain-shadow produced by the rising northern Sierra. The Arcto-Tertiary geofloral pine communities penetrated the peninsula from the north and continued to expand southward as a response to lowering temperatures and the availability of low mountain habitats. Marine temperature data indicate that the winter minimum isotherm for 18° C. now was off the coast of Baja California at about the level of Cabo Colnett (Durham, 1950).

Unfortunately, Pleistocene climate changes and geofloral shifts are not well-known for the far west. Consequently, the patterns during this period must be described less on the basis of paleoecology and paleobotany and more from interpretations of current distributions. It is obvious that temperatures and rainfall have fluctuated in a sequence generally correlated with the advance and retreat of glaciers during the Pleistocene on a continental basis. Deevy (1949) has summarized the evidence for this view for eastern North America. Martin (1958) reviewed the entire problem and provided a resumé of data which established the impact of these changes on western United States and Mexican species. Basically temperature shifts southward at glacial maxima forced temperate elements southward into regions occupied by warm-adapted types during periods of glacial recession. Temperature isotherms and correlated climatic conditions moved as much as 600 miles between glacial maxima and minima (Durham, 1950, 1954) along the west coast with profound local effects in altitudinal displacement. In addition, although rainfall fluctuated during glacial and interglacial stages, throughout the period each succeeding interglacial became more arid than those preceding it. Development of winter rain climate in coastal California and northern Baja California also appears to have taken place during the Pleistocene.

The effects of these three climatic features, temperature fluctuation, trend toward aridity, and the appearance of a winter rain belt, have all significantly modified the herpetofaunal composition of Baja California. Evidence from geofloral records in southern California (Axelrod, 1950) and marine surface temperature data, as well as faunal distribution suggest that two distinctive situations prevailed at glacial versus interglacial times. During interglacial peaks the peninsular ecology did not differ greatly from present conditions. The basic pattern of the late Pliocene was modified by increasing

aridity in the rain-shadow area of the northeast and central regions of the peninsula. These shifts brought about further restriction of the thorn-scrub to the extreme Cape area, domination of most of the peninsula by desert vegetation, and fragmentation of the Madrean woodland-chaparral communities into a northern west coastal unit and a southern Cape upland unit. Increased elevation of the northern ranges allowed the Arcto-Tertiary communities to persist in these montane areas.

At periods of glacial maxima the picture changed markedly. The northern pine woodlands apparently moved somewhat southward and to lower elevations. The oak woodland and chaparral communities seem to have pushed southward and probably became co-extensive with comparable elements advancing northward and to lower elevations from the Cape mountains. Thorn-scrub seems to have maintained itself in the lowlands of the Cape region and possibly extended farther north along the Pacific coast. Desert vegetation was probably replaced by Madrean communities related to sage scrub and chaparral. Desert elements seemed to have survived in marginal thorn-scrub and chaparral areas of maximum temperature and minimal rainfall. At the heights of glacial recession desert conditions were re-established and desert vegetation re-constituted from these marginal communities and from desert immigrants from the Mexican mainland. The theory of desert replacement and re-constitution at glacial maxima and minima applies only to the peninsular region. The evidence a) that at maximum glaciation in the north, climatic conditions in central Baja California resembled those near Los Angeles today (Durham, 1950); b) that Arcto-Tertiary elements shifted far to the southward at this time (Chaney and Mason, 1934); and c) the current nature of the fauna of the central portion of the peninsula, all support this concept.

The apparent disappearance of the central peninsular flora and fauna during the Pleistocene as suggested by Nelson (1921), Johnston (1924), and Beal (1948) also support my concept. These authors invoke a marine flooding of the entire central peninsula to explain the apparent absence of desert communities in the region during glacial peaks. No extensive flooding of this region is satisfactorily demonstrated by geologic evidence (Durham and Allison, 1960) but the climatic changes outlined above indicate that the environment became highly modified and unsuitable for desert forms.

Re-invasion of the most arid segment of the peninsula by desert vegetation from further south along the Mexican mainland is an integral part of my theory. Whether desert conditions persisted in what is now southern Sonora and Sinaloa during the crucial glacial maxima or whether there was a re-constitution of desert vegetation from thorn-scrub and oak woodland and chaparral communities is not clear at present. In any event the most recent post-glacial changes included northward movements of desert vegetation from the Cape region and from the Sonoran desert area to the head of the Gulf of California and thence southward into the peninsula. The thorn-scrub community seems to be stabilized in the Cape lowlands, although an admixture of thorn-scrub and desert elements is typical of certain areas. Retreat of pine woodlands upward on the northern Sierra and restriction of oak woodland and chaparral communities to disjunct elements along the northwest coast and in the southern mountains complete the latest phase of Cenozoic history.

In summary, since the time of the origin of the early peninsula and gulf areas in the Eocene two long-term climatic and vegetational trends have molded the herpetofauna of the region. The first of these trends has been gradual modification of the Eocene tropical climate toward temperate and subtropic conditions. This climatic shift which involved gradual changes up to mid-Miocene has been intensified in the Pliocene and Pleistocene

by the general restriction of the world-wide tropical belt southward (Axelrod, 1952). Vegetational changes associated with the climatic shift have been away from humid tropical vegetation of Neotropical Tertiary floral affinities toward dominance by mid-Miocene of the semi-arid antecedents of Madro-Tertiary components. In addition the temperate Arcto-Tertiary Geoflora invaded the northern region of the peninsula in late Pliocene.

The second major trend has been toward a more arid climate. Increasing aridity seems to have provided the stimulus for the development of characteristic Madro-Tertiary vegetation in western North America and the dominance of Madro-Tertiary derivatives in Baja California today. Rather late in origin have been the distinctive desert vegetational elements, which have lacked community stability in Baja California during the Pleistocene. A minor and probably recent trend has been the restriction of rainfall to the winter months in the northern sections of the peninsula. Summer rains are characteristic of the Cape region and the Peninsular Desert and this difference may explain the persistence of Neotropical Tertiary geofloral elements mixed with the Madro-Tertiary thorn-scrub in southern Baja California (Wiggins, 1960). The Colorado Desert portion of the peninsula has very low rainfall and the rains are concentrated in the winter.

The history of the herpetofauna is closely associated with the physiographic and climatic developments just discussed. As pointed out earlier in this article the several historical elements of the North American herpetofauna are broadly correlated with specific fragments derived from the three Tertiary Geofloras. The scanty available fossil evidence (Gilmore, 1928, 1938; Brattstrom 1955a, 1958a; and Peabody, 1954, 1959) suggests that the associations between herpetofaunal elements and specific geofloral derivatives have existed on a long-term basis and that the same complex of factors has operated in the evolution of modern vegetation and modern herpetofaunas. In any event, an interpretation of the history of the amphibians and reptiles of Baja California requires a reliance upon the well-documented geofloral record.

Baja California in Eocene time was apparently occupied by a herpetofauna associated with the Neotropical Tertiary floral elements of this essentially humid, tropical climatic area. Amphibians and reptiles in the tropical regions of North America at this time were remarkably distinct from recent assemblages in the region, but exhibit definite affinities to the faunas of both present day old and new world tropics. Since the American continents had only recently been separated by the Panamanian portal similar basic groups (families and some genera), probably inhabited both areas. Members of these tropical herpetofaunas belong to a generalized Tropical American unit, discussed in a previous section, which evolved into the basic herpetofauna of late Cenozoic South America. Lying far to the north of Baja California at this time, with its southern limits north of the present Canadian border, was a second major geofloral assemblage, the Arcto-Tertiary, typical of cooler more temperate climatic conditions. Amphibians and reptiles of the Old Northern Element are derived from ancestral forms which inhabited this northern region.

In the Oligocene the first marked changes in climate began to affect western North America. The general changes brought about southward dispersal of Arcto-Tertiary species and among amphibians and reptiles a correlative movement of Old Northern forms in the same direction. These forces had little direct influence on Baja California, except as they laid the basis of changes in the Miocene. Of considerably greater significance, however, was the *in situ* development of the Young Northern Element of the herpetofauna as Madro-Tertiary floral components began to sort out and become evident in this period. The ancestors of most living genera of characteristically

Madrean and Desert and Plains Complexes were originating at this time in savanna and scrub vegetational zones throughout tropical and subtropical portions of North America. The events of post-Oligocene history have given these Young Northern groups dominance in the west to the point where none of the forms in Baja California may be considered pre-Miocene relicts.

In early Miocene times (Fig. 8) Baja California still formed an area dominated by Neotropical Tertiary floral components. The climate appears to have been somewhat cooler and drier than earlier in the Tertiary and dry tropical and subtropical habitats probably predominated. The cognates of the South American Element of the herpetofauna during the period from mid-Eocene to Miocene seem to have been undergoing a gradual evolution into genera and species adapted to more arid and less equable climatic situations than had previously prevailed. This evolutionary challenge probably was correlated with the climatic and vegetational changes giving rise to the Madro-Tertiary Geoflora (Axelrod, 1958) and led to the development of the Young Northern Element of the American herpetofauna by mid-Miocene. Early invaders into Baja California were Young Northern Element forms associated with thorn-scrub communities. Today the remnants of these groups are associated with thorn-scrub vegetation in the Cape region or are isolated on southern islands in the Gulf of California. They include the insular lizards *Sator* and *Cnemidophorus ceralbensis*, the Cape amphisbaenid *Bipes*, and the snake *Eridiphas slevini* which is found on Cerralvo Island and in the Cape area.

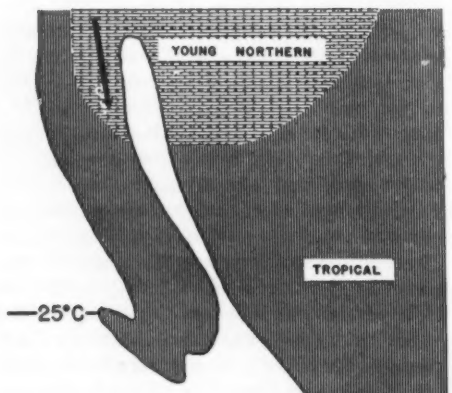

FIG. 8. Distribution of herpetofaunal elements in Baja California region in early Miocene. Location of marine surface minimum winter isotherm of 25° C. indicated. Solid arrow indicates direction of immigration of developing Madrean Complex species, following retreat of tropical types.

Old Northern Element forms ranged farther south at this time than previously, at least into what is now the northern portions of California, Nevada, Arizona, and New Mexico. The herpetofauna of the peninsula in mid-Miocene was essentially of evolving units of the Young Northern Element associated with marginal Neotropical Tertiary floral elements and the Madro-Tertiary Geoflora as it gradually replaced the Neotropical Tertiary over much of the region. The decrease in temperature and increased aridity responsible for floral evolution provided a stimulus to the invasion of the peninsula from the north by additional representatives of the Young Northern Element. By early Pliocene (Fig. 9) the ancestors of dominant peninsular genera were in Baja California. Apparently the herpetofauna was of a generalized composition of Madrean and Desert and Plains Complex types. Among present day inhabitants of the peninsula the following taxa appear to be derived from these Young Northern invaders: *Coleonyx, Phyllodactylus, Xantusia, Ctenosaura, Phrynosoma coronatum, Sceloporus orcutti, Urosaurus microscutatus-*

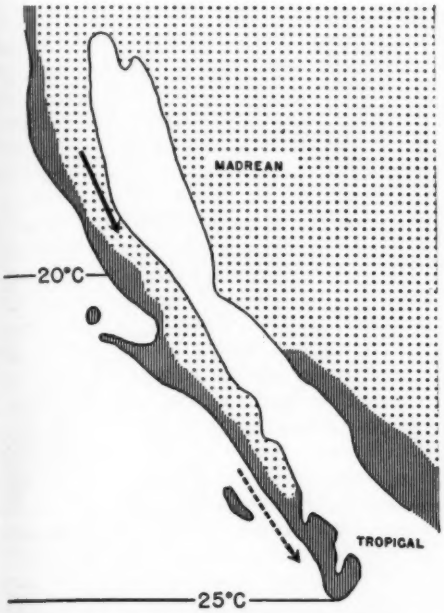

FIG. 9. Distribution of herpetofaunal elements in early Pliocene. Location of minimum winter isotherms for marine surface temperatures indicated. Solid arrow indicates direction of expansion of Madrean Complex species, broken arrow indicates contraction of ranges of more tropical types.

nigricaudus, Uta mearnsi-thalassina, Eumeces, Cnemidophorus hyperythrus, Cnemidophorus maximus, Gerrhonotus, Anniella, Leptotyphlops, Lichanura, Chilomeniscus, Coluber lateralis-aurigulus, Hypsiglena, Pituophis, Sonora, Tantilla, Thamnophis, Trimorphodon, Crotalus enyo and *Crotalus ruber.*

Elsewhere in North America the Arcto-Tertiary Geoflora and associated Old Northern Element continued to expand southward as cooling increased. Apparently at this time or earlier in the Miocene certain warm temperate forms of the Old Northern Element became associated with the remaining thorn-scrub community of Madro-Tertiary vegetation to become established in Baja California (*Pseudemys, Elaphe, Natrix*) and in the case of the first and last genera, in similar subhumid thorn-scrub areas of west Mexico (Fig. 9).

In the Pliocene the effects of mountain building and the acceleration of increasingly arid trends brought about restriction of the relictual Neotropical Tertiary floral units southward. The Madro-Tertiary Geoflora developed into woodland-chaparral and desert components (Axelrod, 1958), as Madrean and Desert and Plains Complexes of the Young Northern Element of the herpetofauna underwent similar diversification. By late Pliocene (Fig. 10) the thorn-scrub persisted in southern Baja California but practically none of its original faunal components survived the competition of the aggressive Madrean invaders. A number of species groups appear to have invaded Baja California from the north at this time from mainland Mexican centers of desert

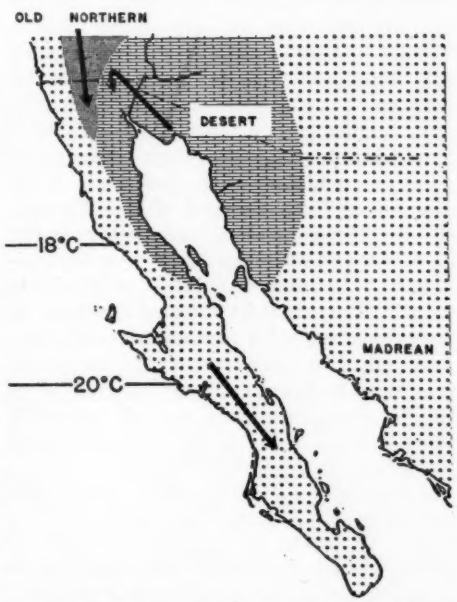

FIG. 10. Distribution of herpetofaunal units in late Pliocene. Solid arrows indicate direction of dispersion of Madrean and Western American Complex species, following southward retreat of thorn-scrub associates of Madrean group. Location of minimum marine surface isotherms indicated.

vegetation to occupy the arid regions of the peninsula. Ancestors of the following groups belonging to the Desert and Plains Complex probably became established in Baja California as a result of this invasion: *Scaphiopus couchii, Bufo punctatus, Callisaurus, Dipsosaurus, Gambelia, Sauromalus, Phyllorhynchus* and *Crotalus mitchellii.* Strictly Arcto-Tertiary associated members of the Old Northern Element (Western American Complex) became established in the montane and relatively humid areas of northwest Baja California at this time and included the ancestral stocks of the following recent groups: *Aneides, Batrachoseps, Ensatina,* and *Clemmys.*

The history of the herpetofauna of Baja California during the Pleistocene is complicated by an inadequate knowledge of the time, number, extent, and climatic influences of glacial correlated change throughout western America. Martin (1958) has surveyed current information and concludes that temperature depression and associated effects were of major significance in the west. Although it is not possible to more than sketch the Pleistocene history of the peninsula, it appears that from the end of the Pliocene onward three trends already begun in the Miocene and Pliocene have been intensified: a) decrease in rainfall with winter rain in the north; b) general decrease in temperatures, with temperate conditions established in the north; and c) increased mountain-building. These trends continued throughout the period but with temporal shifts due to the fluctuations of glacial and interglacial climates.

Apparently (Axelrod, 1957) three glacial cycles had major effects in the far west. In each succeeding interglacial period aridity increased. Although exact dating is not possible the general patterns at glacial maxima and minima have been outlined previously.

At times of glacial maxima (Fig. 11) temperatures became lowered and humidity increased. Under these circumstances thorn-scrub communities re-

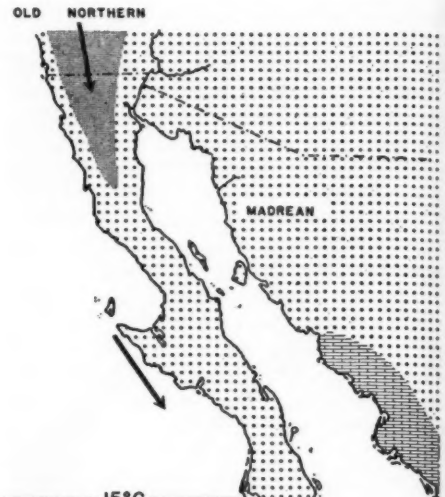

FIG. 11. Distribution of herpetofaunal complexes in Baja California at times of glacial maximum in Pleistocene. Solid arrows indicate direction of dispersion into peninsula from north, broken arrows the retreat of desert and thorn-scrub associates southward. Note the location of the minimum winter isotherm for marine surface temperature at level of Bahia Magdalena, which corresponds to situation near San Diego today.

treated and persisted only in the extreme southern Cape areas. Subhumid coniferous woodlands expanded in the northwest coastal and montane area. Oak woodland-chaparral communities dominated the entire central peninsula and scrub vegetation probably covered the northeast arid area as well. Madrean forms with relatively high rainfall requirements (*Scaphiopus hammondii, Bufo microscaphus,* and *Hyla arenicolor*) probably invaded the moister coastal regions from the north at this time. Two members of the Holarctic Element (*Bufo boreas* and *Rana aurora*) also became established in the nothern portions of the peninsula.

Madrean Complex species of the Young Northern Element dominated in central

Baja California but desert forms were mostly restricted to the south in a thorn-scrub refugium in the Cape. Example species in the former category include forms which today make up the distinctive San Lucan and California Components: *Scaphiopus hammondii, Bufo microscaphus, Hyla arenicolor, Hyla regilla, Phrynosoma coronatum, Eumeces, Cnemidophorus labialis, Gerrhonotus, Anniella, Leptotyphlops, Coluber lateralis-aurigulus, Hypsiglena, Lampropeltis getulus, L. zonata, Diadophis, Pituophis, Tantilla,* and *Thamnophis.* Desert species of the Desert and Plains Complex restricted at glacial maxima into a thorn-scrub refugium in Southern Baja California included ancestors of the following: *Scaphiopus couchii, Bufo punctatus, Coleonyx, Callisaurus, Dipsosaurus, Sauromalus, Sceloporus orcutii, Cnemidophorus maximus, Chilomeniscus, Phyllorhynchus, Crotalus enyo,* and *Crotalus ruber.* At which interglacial period the fragmentation typical of each of these desert species groups occurred is problematical. In most of the cited examples a related geographical race or species seems to have developed from forms in a similar refugium region for Sonoran Desert representatives in western Mexico. Evidence from other sources indicates that Chihuahua desert species were also displaced southward at glacial peaks and probably survived in a scrub refugium during these periods (Fig. 13). In any event the evidence is strong that desert environments were all but eliminated in Baja California during certain times in the Pleistocene and that reconstitution of desert herpetofaunas occurred at glacial minima by invasion of the peninsular desert from the south (Cape refugium) and from the north by forms that had immigrated northward around the head of the Gulf of California from the Sonoran refugium. Recent northern invaders falling into this group include the following examples: *Crotaphytus, Phrynosoma platyrhinos, Sauromalus obesus, Sceloporus magister, Urosaurus ornatus, Cnemidophorus tigris, Arizona elegans,*

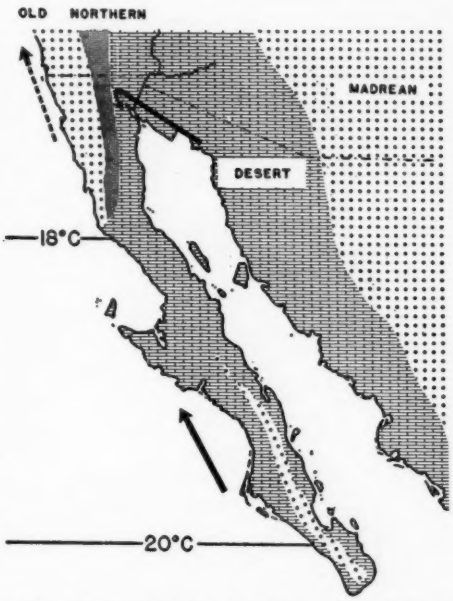

FIG. 12. Distribution of herpetofaunal complexes in Baja California at interglacial times. Solid arrows indicate direction of expansion by Desert and Plains Complex, broken arrow retreat of Madrean Complex. Location of marine surface isotherms for February indicated.

Sonora semiannulata, and *Crotalus atrox.*

As temperatures and aridity increased (Fig. 12) during Interglacials desert vegetation and herpetofauna replaced the oak woodland-chaparral communities and Madrean herpetofauna except in the Californian and San Lucan areas. Fragmented ranges and origin of paired allopatric species (Fig. 14) in the California and San Lucan regions, separated by 300 miles of desert, have been the result. The desert zones in mid-peninsula were invaded by warm arid adapted forms from the Cape thorn-scrub refugium and by species moving around the Gulf of California from the mainland region as desert conditions expanded. A number of species beautifully illustrate the dual invasion of the central area (Fig. 15). Persistence of temperate faunal elements in the north even at glacial minima is apparently explained by

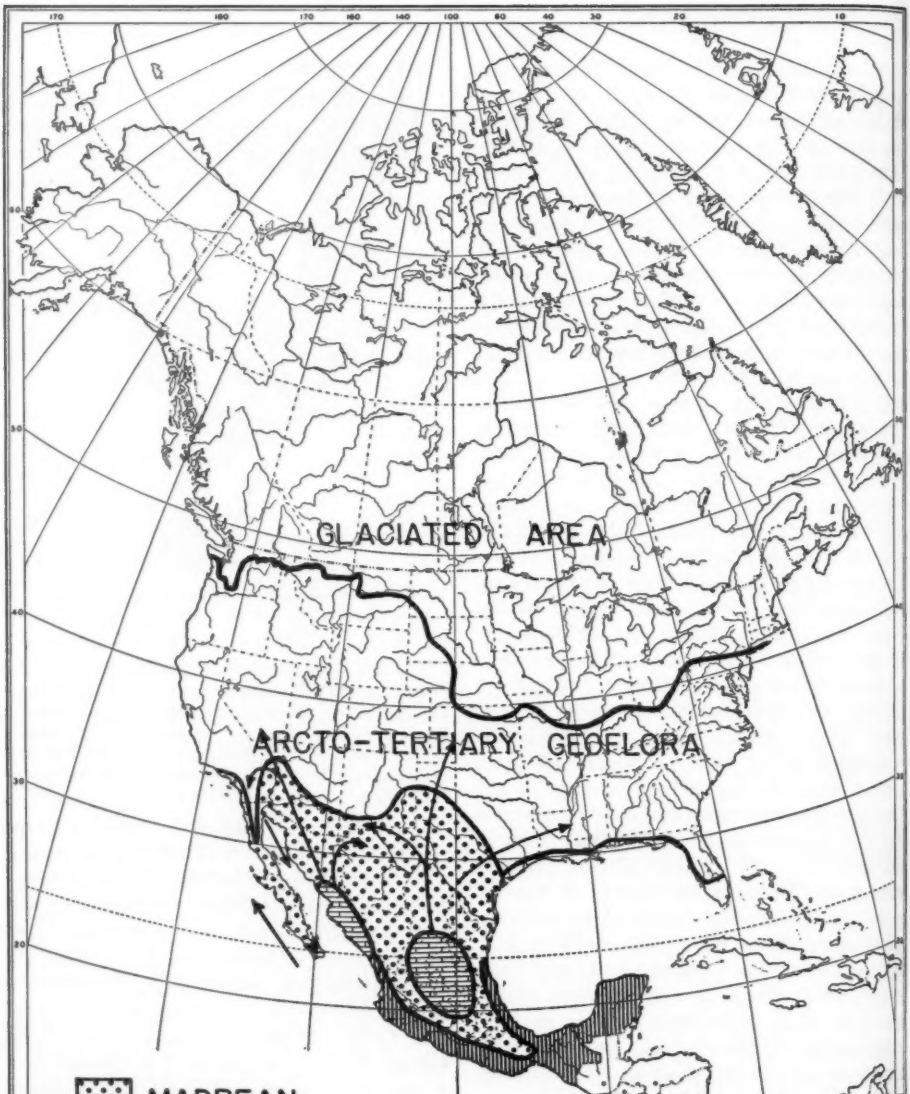

FIG. 13. Distributional pattern of herpetofaunal elements in North America at glacial maxima to indicate probable location of refugia for desert forms. Solid arrows indicate the general direction of dispersion for desert forms as glaciers retreated and arid conditions made more northern areas available for occupancy.

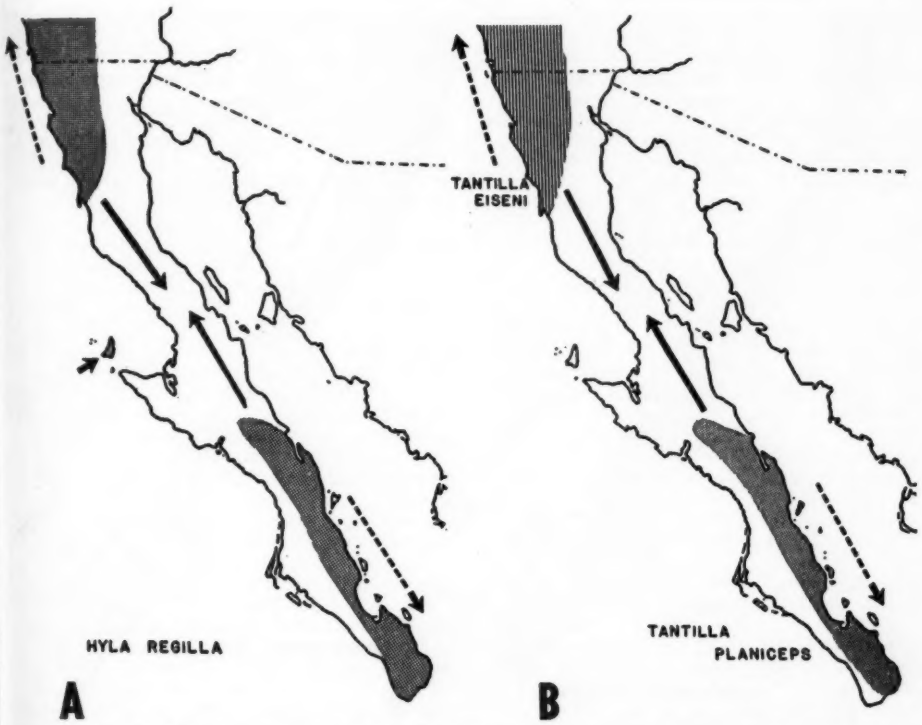

FIG. 14. Distribution patterns indicating interglacial fragmentation of continuous ranges of Madrean Complex fauna in Baja California. A. Range of the western treetoad, *Hyla regilla*. B. Range of California black-headed snake, *Tantilla eiseni* and San Lucan black-headed snake, *Tantilla planiceps*. Solid arrows indicate direction of dispersion by these forms at glacial maxima, broken arrows the contraction of ranges in interglacial periods.

the continued elevation of the northern Sierra.

Summary

Historically, the peninsular region has been invaded by four waves of immigrants from the north that have all but replaced the early Tertiary fauna of the area. The first wave consisted of groups of the Madrean Complex of the Young Northern Element which came to dominate the herpetofauna in the Pliocene. These groups invaded the peninsula from the north and ultimately formed the basic fauna of the Californian and San Lucan areas. Initial invasion correlated with lowering of temperatures and the development in the peninsula of Madro-Tertiary floral types. A second wave of desert adapted groups came into northern areas during the Pliocene as aridity increased. General temperature decreases in the northern Sierra montane area and increased elevation allowed a third wave of Arcto-Tertiary association to penetrate into Baja California concurrent with desert formation in the east and south. In the Pleistocene a second wave or even several waves of desert forms invaded the peninsula from the northeast at times of interglacial conditions.

Events in the Pleistocene culminated in increased elevation of the mountains, increased aridity, and general temperature

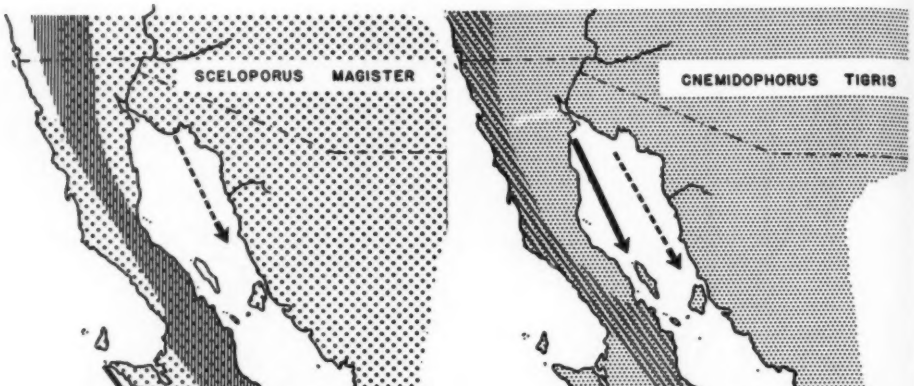

FIG. 15. Distribution patterns indicating dual invasion of Peninsular Desert area from north and south during postglacial periods. A. Ranges of desert scaly lizard, *Sceloporus magister*, and granite scaly lizard, *Sceloporus orcutti*. B. Ranges of orange-throated whiptail, *Cnemidophorus hyperythrus*, and western whiptail, *Cnemidophorus tigris*. Solid arrows indicate current, postglacial, direction of dispersion, broken arrows the contraction of ranges during glacial maxima.

depression. At glacial maxima Madrean Complex groups dominated most of the peninsula, with Desert and Plains Complex groups restricted to a Cape refugium. Similar restriction of arid adapted forms on the Mexican mainland to a southern refuge laid the basis for interglacial invasion of the peninsula by Mexican desert elements as Madrean groups were eliminated from central Baja California. Species from the Cape refugium also moved northward into developing desert areas so that the modern Peninsular Desert Fauna is a mixture of Cape forms and Mexican mainland types that moved around the head of the Gulf of California to invade Baja California. Madrean Complex species are now restricted to two disjunct areas: a) the northwest coastal and montane area and b) the San Lucan uplands. Northern mountain areas continue to support cooler adapted species because of continued uplift and higher rainfall conditions.

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The Fresh-water Fishes—Their Origins and Affinities

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Introduction

THE INDIGENOUS fishes that are known from fresh water in Baja California are referable to 17 families, 25 genera, and 29 species. All but *Xyrauchen, Gila, Ptychocheilus,* and perhaps *Cyprinodon,* are of marine affinities. The single endemic species is *Fundulus lima.*

With the exception of the one endemic species, there exists no such discrete assemblage of fishes as might strictly be designated the fresh-water fauna of Baja California. Four reasons for the absence of such a fauna are evident:

1. A discontinuity between certain coastal streams of southern California and the Tijuana River has prevented the fresh-water fishes of the Santa Ana system from extending farther south than the San Luis Rey River, San Diego County, California (see Culver and Hubbs, 1917:82). This restriction of the Santa Ana fauna suggests that the streams of that system were not connected with the Tijuana River or with streams farther south, during Pleistocene lowering of sea level.

2. Aridity, apparently of long standing, has prevented the coastwise dispersal of fishes by way of estuaries.

3. The abrupt escarpment along much of the eastern shore nearly precludes the formation of lagoons, which might have facilitated dispersal.

4. The Gulf of California is a barrier to the entry of fresh-water fishes from Middle America. (See p. 31, infra, for Middle American species erroneously recorded from Baja California.)

For these reasons, the fishes recorded from fresh water in Baja California are limited to various marine derivatives, except for the few strictly fresh-water species which (until extirpated by the white man) constituted the depauperate but highly specialized fauna of the lower Colorado River.

Origins

The fishes known from fresh water in Baja California represent dispersals from five distinct faunal areas:

1. From the northeastern Pacific coast, a southward dispersal of three euryhaline species:

Salmonidae

Salmo gairdnerii. Several records.

Cottidae

Leptocottus armatus australis. Two records.

Gasterosteidae

Gasterosteus aculeatus microcephalus. Several records.

2. From the lower Colorado River, a southward (downstream) dispersal of three species:

Catostomidae

Xyrauchen texanus. Several records.

Cyprinidae

Gila robusta elegans. Several records.
Ptychocheilus lucius. Several records.

3. From the lowlands of the Atlantic seaboard and adjacent regions (basically), a westward dispersal of three species:

Cyprinodontidae

Fundulus parvipinnis parvipinnis. Several records.
Fundulus lima. Several records.
Cyprinodon macularius. Several records.

4. From the Gulf of California, an occasional entry into fresh water in the distributaries of the Colorado River, by three species apparently restricted to the Gulf:

Sciaenidae

Micropogon megalops. One report.
Cynoscion xanthulus. One report.
Cynoscion macdonaldi. One report.

5. From the Panamic region, a northwestward dispersal of 17 species, five of which have passed beyond the boundaries of Baja California—*Gillichthys mirabilis* to the extent that it is more appropriately included in the Californian fauna:

Elopidae

Elops affinis. Three hypothetical records.

Bothidae

Citharichthys gilberti. One record.

Centropomidae

Centropomus nigrescens. One report.

Mugilidae

Mugil cephalus. Several records.
Mugil curema. Three records.
Agonostomus monticola. Two records.

Gerridae

Eucinostomus gracilis. Two records.
Gerres cinereus. One record.

Lutjanidae

Lutjanus novemfasciatus. One record.
Lutjanus argentiventris. One report.

Haemulidae

Pomadasys bayanus. One record.

Syngnathidae

Pseudophallus starksii. One record.

Eleotridae

Gobiomorus maculatus. Two records.
Dormitator latifrons. Several records.
Eleotris picta. Several records.

Gobiidae

Awaous transandeanus. Several records.
Gillichthys mirabilis. Three records.

The indigenous fresh-water fishes of Baja California constitute an essentially peripheral fauna. The Holarctic genus *Salmo* has reached its southwesterly limits in Arroyo del Rosario (although it has extended farther south on the Mexican mainland). The northeastern Pacific genus *Leptocottus* has reached its southerly fresh-water limits at Arroyo San Miguel. The Holarctic family Gasterosteidae has reached its southerly limits in western North America approximately at El Rosario. One species of the principally Nearctic family Catostomidae and two

species of the widespread family Cyprinidae have reached in the distributaries of the Colorado River the southernmost limits of their range. The temperate genus *Fundulus* has reached its southwesterly fresh-water limits in the southern part of Baja California. The New World genus *Cyprinodon* has reached in northeastern Baja California the westerly limits of its range. On the other hand, representatives of the tropical genera *Agonostomus, Pomadasys, Pseudophallus, Gobiomorus, Dormitator,* and *Awaous* have reached their northwesterly limits at or near Cabo San Lucas.

Representatives of the Elopidae, Bothidae, Centropomidae, Lutjanidae, Eleotridae, and Gobiidae are the Pacific representatives of geminate species (see Jordan, 1908); they are apparently reminiscent of a wider, continuous distribution of their ancestral forms, which may have prevailed before the seaway connecting the Atlantic and Pacific oceans was closed at the end of the Miocene (see Olsson, 1932:39, 43).[1]

Analysis of the Species

In the following analysis of the fresh-water fishes of Baja California, a general statement of the distribution of the family is followed by comments on the affinities, distribution, and fresh-water status (salt tolerance) of each species concerned, and by an enumeration of the records or reports of the occurrence of that species in fresh water in Baja California.

Six categories of fresh-water status, based on the salt-tolerance classification proposed by Myers (1951:12), are employed:

Primary: Strictly intolerant of salt sea water.

Secondary: Rather strictly confined to fresh water, but evidently capable of occasionally crossing narrow sea barriers; many with known tolerance of sea water for short periods.

Diadromous: Regularly migratory between fresh and salt water at a definite period of the life cycle.

Vicarious: Presumably nondiadromous fresh-water representatives of partly or primarily marine groups.

Complementary: Marine-group representatives, often or usually diadromous, that become dominant in fresh water only in the paucity or absence of primary, secondary, and probably also vicarious, fresh-water faunas.

Sporadic: Fishes which live and breed indifferently in salt or fresh water or which enter fresh water only sporadically and not as a part of a true migration.

Elopidae—Tarpons

The fishes of this family, which are considered the most archaic of existing teleosts (Ridewood, 1904:54), are of circumtropical distribution (Regan, 1909).

Elops affinis Regan, 1909

Affinities. The higher gillraker count distinguishes this fish from its geminate species, *Elops saurus* Linnaeus, 1766, of the Atlantic coast of the Americas (Regan, 1909:38; Hildebrand, 1943:91).

Distribution. Salton Sea, California (Dill and Woodhull, 1942:171), to Isla Lobos de Tierra, Peru (Hildebrand, 1946:79).

Fresh-water status. Sporadic. This marine species enters fresh water, as do others of its genus (Boulenger, 1909: 25–27; Gunter, 1942:313). In the Colorado River, it appears so rarely in fresh water as to seem referable to the sporadic group rather than to the diadromous group (cf. Miller, 1958:188).

Baja California fresh-water records. The statement that this species passes through the entire Mexican part of the Colorado

[1] Olsson included the Pontian of Europe in the Miocene, but North American vertebrate paleontologists refer the Pontian to the lower Pliocene. Therefore latest Miocene in Olsson's terminology is lower Pliocene in the terminology of most North American vertebrate paleontologists (J. Wyatt Durham, personal communication).

River (de Buen, 1947:310) is corroborated by three records from California (and was presumably based on the earlier two): Colorado River at Laguna Dam (Glidden, 1941:272); Salton Sea (Dill and Woodhull, 1942:171); and Colorado River at Imperial Dam, November 1958 (Leo Shapovalov, in litt.).

Salmonidae—Trouts

This family, of marine origin (Regan, 1906–1908:176), is essentially north temperate and subarctic in distribution (Dymond and Vladykov, 1934:3748).

Salmo gairdnerii Richardson, 1836

Affinities. Trout from the west slope of the Sierra San Pedro Mártir have been regarded as a distinct species, *Salmo nelsoni* Evermann (1908:26); as a "geographically isolated form of the rainbow trout" (Snyder, 1926:419); as a possibly distinct subspecies (Miller, 1950:29); and as undifferentiated, even subspecifically (Hubbs, 1946:84; Needham and Gard, 1959:44).

Distribution. Kuskokwim River, Alaska, to Río Presidio, Durango, Mexico (Needham and Gard, 1959:11, 60). This species may have been introduced into the Río Presidio, but it is surely native in the Río Fuerte, where it is represented by a distinctive form, described (but not named) by Needham and Gard (1959:50–57).

Fresh-water status. Diadromous, but with many landlocked stocks.

Baja California fresh-water records. Arroyo San Antonio, tributary to the Arroyo Santo Domingo (Arroyo San Ramón), west slope of Sierra San Pedro Mártir, elevation about 2,000 feet (Meek, 1904:96, as *Salmo irideus.* Evermann, 1908:26; Nelson, 1922:22, 80, 134; Snyder, 1926, as *Salmo nelsoni,* Myers, 1930:101, as *Salmo irideus.* Needham, 1938, as *Salmo nelsoni.* Hubbs, 1946:84, as *Salmo gairdnerii irideus.* Hubbs, 1948:463; Miller, 1950:29; as *Salmo gairdnerii nelsoni.* Needham and Gard, 1959:44, as *Salmo gairdnerii.* Calif. Acad. Sci. Nos. 21222–21224).

Under primitive conditions, oceanic migrants probably ascended the Tijuana River into Baja California, since they are known from the lower course of that stream, in California (Hubbs, 1946:83). Such migrants have been reported from as far south as Arroyo del Rosario (Carl L. Hubbs, personal communication).

The presence of trout in the following streams of Baja California apparently resulted from introduction by man, and is therefore without zoogeographic significance: Arroyo San Jacinto (a tributary of Arroyo San Vicente) and Arroyo San Rafael (trout introduced from Arroyo Santo Domingo; Needham and Gard, 1959: 46); Boca de la Sierra, tributary to Arroyo San José, some 25 miles above San José del Cabo (trout observed, January 19, 1959; Hugh B. Leech, personal communication).

Catostomidae—Suckers

It has been said that this family appears to have originated in the vicinity of India and to have reached North America across Bering Strait during a recession of sea level before the Eocene (Regan, 1922:207). However, the earliest reliably dated remains of the family in North America are from Miocene deposits (Miller, 1958:201). This family has a single representative in China and another in northeastern Siberia, but has developed extensively in North America, where it is widely distributed (Miller, 1958:199–203, Fig. 10). It has been inadvertently shown as occupying all of Baja California (Regan, 1906–1908:xxiii, Catostominae).

Xyrauchen texanus (Abbott, 1860)

Affinities. Osteological characters (Nelson, 1948:241; 1949:563) and natural hybridization (Hubbs and Miller, 1953:226) indicate that the relationships of this sucker are with *Catostomus.*

Distribution. Colorado River system (Dill, 1944:150).

Fresh-water status. Primary.

Baja California records. Colorado River from Yuma, Arizona, to Horseshoe Bend, below Lerdo, Mexico; "Hardee's Colorado" (Gilbert and Scofield, 1898:491). Río Hardy (Fowler, 1913:55). A laguna of Salton River[2] at Seven Wells (south of monument No. 213, M.B.L.), about four miles south of the United States border, April 14 and 15, 1894 (Edgar A. Mearns, unpublished field notes, as *Catostomus cypho*).

Cyprinidae—Minnows

This family has been said to have originated in southern Asia and to have reached North America across Bering Strait at the time of a recession of sea level during the Oligocene (Regan, 1922: 207). Recently, however, the paleontological evidence has been said to indicate that minnows reached North America not prior to the Miocene (Miller, 1958:203).

The Cyprinidae are widely distributed in Asia, Africa, Europe, the Malay Archipelago west of Makassar Strait, and North America (Weber and de Beaufort, 1916: 44; Myers, 1951:13). They have inadvertently been shown as occupying all of Baja California (Regan, 1906–1908:xxiv, Cyprininae; Norman, 1931: Fig. 101).

Gila robusta elegans Baird and Girard, 1853

Affinities. Forms related to this highly specialized minnow occur in the Colorado River system (Miller, 1946:414). Congeneric species are known from the Klamath River system, the Bonneville basin and upper Snake River, the Sacramento-San Joaquin system, streams of the Santa Ana system of southern California, the Río Grande, the Río Yaqui, and the Río de la Concepción (Miller, 1945).

Distribution. Colorado River system (Miller, 1945:104).

Fresh-water status. Primary.

Baja California records. Colorado River at Horseshoe Bend (Gilbert and Scofield, 1898:492, as *Gila elegans*). "Salton River, Colorado Desert, Lower California" (Snyder, 1915:581, as *Gila elegans*). The Salton River record was apparently based on the unpublished field notes of Edgar A. Mearns, which recorded specimens (as *Gila gracilis* or as *Gila* sp.) from a laguna of the Salton River[2] at Seven Wells (south of monument No. 213, M.B.L.), about four miles south of the United States boundary, April 8–13, 1894. Further evidence of the former occurrence of this minnow in Baja California is provided by skeletal remains collected at Travertine Rock, Imperial County, California, on the beach line of ancient Lake LeConte (Hubbs and Miller, 1948:107, as *Gila robusta*), which at one time extended approximately 17 miles south of the present international boundary and was connected with the Colorado River by channels lying within the area now embraced by Baja California.

Ptychocheilus lucius Girard, 1856

Affinities. Species with which this huge minnow is currently regarded as congeneric occur in the Skeena, Fraser, and Columbia systems, the Puget Sound drainage, coastal streams of Washington, the Siuslaw and Umpqua rivers of Oregon, and the Sacramento-San Joaquin system (Carl and Clemens, 1948:82; Schultz and DeLacy, 1935:378–379; Snyder, 1908:170; Rostlund, 1952:270–271).

Distribution. Colorado River drainage (Ellis, 1914:55).

Fresh-water status. Primary.

Baja California records. Colorado River

[2] Regarding this "Salton River," presumably the present Alamo River, not Salton Creek (a present tributary to Salton Sea), Mearns wrote in his notes: "Salton River is a long slough of the Colorado River, which latter overflows its banks periodically so that the water backs up occasionally as far as the so-called 'Salton Sea,' north of the boundary. New River is similar, farther west." Mearns reported *Xyrauchen texanus, Cyprinus carpio, Gila robusta elegans,* and *Ptychocheilus lucius* from this "river," and described what was probably *Cyprinodon macularius* from there.

at Horseshoe Bend (Gilbert and Scofield, 1898:492). Colorado River "from Ft. Mojave to the Gulf"; laguna of the Salton River,[2] about four miles south of the United States boundary, April 13, 1894 (Edgar A. Mearns, unpublished field notes, as "Colorado Salmon" or as "Verde or Gila Salmon"). Skeletal remains recorded from Travertine Rock, Imperial County, California, on the beach line of ancient Lake LeConte (Hubbs and Miller, 1948:107), provide further evidence of the former occurrence of this species in Baja California, since the ancient lake extended south of the present international boundary and was connected with the Colorado River by channels in Baja California.

Cyprinodontidae—Killifishes

This family extends widely across North and South America, southern Europe, Africa, Asia, and the Indo-Malayan Archipelago (Berg, 1940:464; Meek, 1916: Fig. 67).

Fundulus parvipinnis parvipinnis Girard, 1854

Affinities. This is one of the two Pacific species of a genus which has its center of abundance in the southeastern United States but which, earlier in Cenozoic time, was represented west of the present Continental Divide by at least five species (Miller, 1958:215). The recognition of a distinct subspecies, *Fundulus parvipinnis brevis* Osburn and Nichols, 1916, from Bahía Magdalena, Baja California, was supported by Myers (1930:96).

Distribution. Morro Bay, California (Barnhart, 1936: 22, as *Fundulus parvipinnis*), to Arroyo Carmen, 7.6 miles north of Ensenada, Baja California (Miller, 1943a:51). Erroneously recorded by Jordan and Gilbert (1882a:355) from Cabo San Lucas (Miller and Hubbs, 1954:234).

Fresh-water status. Sporadic. Although this subspecies rather freely enters fresh water (Eigenmann, 1892:142; Miller, 1939: 168; records, infra), I regard it as sporadic because it is preponderantly marine. This species was placed in the secondary category by Miller (1958:215).

Baja California fresh-water records. Arroyo Médano, 2.5 miles north of Arroyo Descanso (Univ. Michigan Mus. Zool. No. 144456); Arroyo San Miguel, about one-half mile above mouth (Univ. Michigan Mus. Zool. No. 144455). Arroyo Guadalupe [= Arroyo San Miguel], about 41 miles south of Tijuana; Arroyo Carmen, 7.6 miles north of Ensenada (Miller, 1943a: 51).

Fundulus lima Vaillant, 1894

Affinities. This is the only endemic species of fish known from fresh water in Baja California. The suggestion by Myers (1930:99) that *Fundulus lima* is a landlocked derivative of *Fundulus parvipinnis* was supported by Miller (1943a: 52).

Distribution. Known only from Baja California; see records, infra.

Fresh-water status. Vicarious. Known only from fresh water. This species was placed in the secondary group by Miller (1958:215), but its very close relationship to *Fundulus parvipinnis* seems to make its reference to the vicarious group more logical.

Baja California records. San Ignacio (Vaillant, 1894:72; Evermann, 1908:26, as *Fundulus meeki;* Myers, 1930:95). Lagoon 22 miles northeast of Comondú (California Acad. Sci. No. 21225). Creek near Carmel, between Canipolé and Comondú (Stanford Natur. Hist. Mus. No. 24565). Comondú (Stanford Natur. Hist. Mus. No. 24563). Arroyo de la Purísima: 13 miles east of La Purísima (Stanford Natur. Hist. Mus. No. 14909); five miles above La Purísima; La Purísima Canyon, 23 miles north of Comondú (Carl L. Hubbs, personal communication); San Isidro (Univ. Michigan Mus. Zool. No. 159267).

Cyprinodon macularius Baird and Girard, 1853

Affinities. This species, a representative of a genus which is presumably of ancient Atlantic coast origin but which is rather well represented in the arid regions of western North America, is a close relative of *Cyprinodon nevadensis* Eigenmann and Eigenmann, 1889, of the Amargosa River (Death Valley) drainage (Miller, 1943b:1). However, it may be even more closely related to the eastern species of this genus (Miller, 1948:22).

Distribution. Drainage basin of the lower Colorado River, including distributaries, from southern Arizona to northeastern Baja California, and the Río Sonoyta of northwestern Sonora, México (Miller, 1948:22).

Fresh-water status. Secondary. Unknown from the ocean, but freely occupying mineralized springs and lakes, including Salton Sea.

Baja California records. Pozo del Tule, northwestern edge of Laguna Salada, about 23 miles west-southwest of Mexicali; Pozo del Cerro Prieto, about 34 miles south of Mexicali; Rancho Agua Caliente (not the town of the same name), three miles southeast of Cerro Prieto; a laguna about five road miles east of Rancho Agua Caliente; and a pool two miles south and 3.5 miles east of Rancho Agua Caliente (Miller, 1943b:17–18). "Ten (10) small fishes from a 'laguna' of Salton River,[2] at Seven Wells, Colorado Desert, Lower California, about four (4) miles south of the U. S. border, April 8, 1894. Color blue, with gold spots on sides of tail, and yellowish caudal fin" (Edgar A. Mearns, unpublished field notes); this description suggests with high probability the male of *Cyprinodon macularius* (see Miller, 1948:24). Hot spring midway of the eastern margin of Laguna Salada, or Laguna Maquata (Jordan and Richardson, 1907: 319, as *Lucania browni;* MacDougal, 1907: 723, as *Lucania brownii*). The temperature of this spring was stated by Jordan and Richardson (1907:319) to have been 128° F., and by MacDougal (1907:723) to have been 112° F. to 128° F. The reported temperature of 128° F. has been doubted; Miller (1948:131), after correspondence with the collector, wrote the temperature as 120° F., with the comment, ". . . it is questionable whether the fish were actually swimming in water of that temperature." This spring is now cooler and shows a strong vertical gradient in temperature; *Cyprinodon* no longer occurs there, or in Pozo del Tule (Carl L. Hubbs, personal communication). Pattie Basin, the site of these two springs, is intermittently populated by distributary overflow from the Colorado River (Hubbs and Miller, 1948:113).

Bothidae—Lefteyed Flounders

This family is widely distributed in tropical and temperate seas (Norman, 1934:48).

Citharichthys gilberti Jenkins and Evermann, 1889

Affinities. This flounder is very closely related to *Citharichthys spilopterus* Günther, 1862, of the Atlantic coast of the Americas—which, in turn, is closely related to *Citharichthys stampflii* (Steindachner, 1894), of tropical West Africa (Norman, 1934:149–152).

Distribution. Laguna Santa María (vicinity of Cabo San Lázaro), Baja California (Calif. Acad. Sci. No. 21226), and Gulf of California (Jenkins and Evermann, 1889:158), to Sullana, Peru (Eigenmann, 1922:218).

Fresh-water status. Sporadic. Like the closely related species mentioned, *Citharichthys gilberti* occasionally ranges into fresh water.

Baja California fresh-water record. San José del Cabo (Osburn and Nichols, 1916: 180).

Centropomidae—Snooks

The species of this family are found in tropical or subtropical American waters (Walford, 1937:126).

Centropomus nigrescens Günther, 1864

Affinities. A geminate relationship between *Centropomus viridis* Lockington, 1877 (= *Centropomus nigrescens;* see Meek and Hildebrand, 1925:428), and *Centropomus undecimalis* (Bloch, 1792), of the Atlantic coast of tropical America, was remarked by Jordan (1908:76). However, *Centropomus nigrescens* and *Centropomus undecimalis* have been regarded as scarcely separable (Meek and Hildebrand, 1925:428).

Distribution. Isla Asunción, Baja California (Lockington, 1877:110, as *Centropomus viridis*), and Gulf of California (see record, infra), to Paita, Perú (Hildebrand, 1946:229).

Fresh-water status. Sporadic. This species frequently enters fresh water (Meek and Hildebrand, 1925:428).

Baja California fresh-water record. Reported taken in fresh water in the laguna at the mouth of Arroyo Mulegé (Boyd W. Walker, personal communication).

Mugilidae—Mullets

This family is widely distributed in warm and temperate seas (Berg, 1940: 469).

Mugil cephalus Linnaeus, 1758

Affinities. This mullet appears to represent a single species of world-wide distribution in tropical and subtropical seas (Meek and Hildebrand, 1923:276; Jordan and Hubbs, 1925:208). It is closely related to *Mugil rammelsbergii* Tschudi, 1845, and possibly to *Mugil peruanus* Hildebrand, 1946, of the eastern Pacific (Ebeling, 1957:173).

Fresh-water status. Sporadic, with strong approach toward diadromy. The young, after attaining the silvery querimana stage in the Gulf, move in immense numbers up the Colorado River, where they often develop into yearlings before returning to the Gulf. In Salton Sea the mullet formerly became very abundant and grew to a large size, but did not reproduce (Carl L. Hubbs, personal communication). The species might therefore be regarded as intermediate between sporadic and diadromous; however, it was apparently regarded as diadromous by Miller (1958:189).

Distribution. Warmer shores of both hemispheres (Meek and Hildebrand, 1923: 276). In the eastern Pacific it is known from San Francisco, California (Jordan and Jouy, 1881:13, as *Mugil mexicanus*), to Puerto Montt, Chile (Mann, 1954:201).

Baja California fresh-water records. Laguna Maquata (Orcutt, 1890:914, and 1891:159, as *Mugil mexicanus*). San José del Cabo (Rutter, 1896:264, as *Mugil albula;* Wales, 1932:165—in fresh water, fide Ira L. Wiggins, personal communication). Arroyo de la Purísima (de Buen, 1942:44). Arroyo San Miguel, one-half mile from ocean (Univ. Michigan Mus. Zool. No. 129587). Colorado River at Horseshoe Bend (Stanford Natur. Hist. Mus. No. 3838). Colorado and Hardy rivers from their junction to a point ten miles above the mouth of the Colorado River (Carl L. Hubbs, personal communication). De Buen (1947:281) said of this species, "Remonta el río Colorado." This statement is corroborated by records from Salton Sea and the Colorado River, in California (Evermann, 1916:62; Thompson and Bryant, 1920:60; Coleman, 1929: 226; and Dill, 1944:163).

Mugil curema Valenciennes *in* Cuvier and Valenciennes, 1836 [3]

Affinities. Closely related to *Mugil setosus* Gilbert, 1892, and *Mugil hospes* Jordan and Culver, 1895, of the eastern Pacific (Ebeling, 1957:173). This species

[3] Names originally published in the work entitled "Histoire Naturelle des Poissons," 1828–1850, that have long been ascribed jointly to Cuvier and Valenciennes "are to be attributed to Cuvier *in* Cuvier & Valenciennes, or, as the case may be, to Valenciennes *in* Cuvier & Valenciennes," in accordance with the tables set forth in Opinion 580 (International Commission on Zoological Nomenclature, 1959: 148).

has been referred to *Mugil brasiliensis* by a number of earlier authors, but it is not identical with *Mugil brasiliensis* Agassiz, 1829 (Jordan and Swain, 1884:269).

Distribution. Both coasts of America, and West Africa (Meek and Hildebrand, 1923:280). In the eastern Pacific, from Bahía de Sebastián Vizcaíno, Baja California (Boyd W. Walker, personal communication), and Gulf of California (Evermann and Jenkins, 1891:136), to Coquimbo, Chile (Mann, 1954:50; but see op. cit.:199, "Iquique y probablemente más al Sur").

Fresh-water status. Sporadic, with less tendency toward diadromy than shown by *Mugil cephalus.*

Baja California fresh-water records. Arroyo San José, San José del Cabo (Jordan and Gilbert, 1882b:379, as *Mugil brasiliensis;* Rutter, 1896:264; Osburn and Nichols, 1916:158).

Agonostomus monticola (Bancroft *in* Griffith and Smith, 1834)

Affinities. Formerly considered distinguishable from *Agonostomus nasutus* Günther, 1861, by the shape of the snout (Regan, 1906–1908:66). Later the two were regarded as identical (Meek and Hildebrand, 1916:335). Pending further study, I follow Hubbs (1953b:146) in accepting the later interpretation. A number of species of *Agonostomus* have been recognized from tropical America (cf. Regan, 1906–1908:66; Seale, 1932:467; Hubbs, 1953b:146), but it cannot be said with confidence that they are distinct from *Agonostomus monticola.*

Pending thorough study of the mountain mullets, I refer the American species to the genus *Agonostomus* (cf. Hubbs, 1953b:146). That genus has been said to range from the tropical New World westward to the Hawaiian Islands (Hawaiian record [4] based on a single specimen, (New Zealand, New South Wales, and Mauritius (Schultz, 1946:379, 385). However, there appears to be good reason for regarding the representative of New Zealand and Australia, *Agonostomus forsteri* (Valenciennes *in* Cuvier and Valenciennes, 1836),[3] as referable to a distinct genus (Thomson, 1954:88). Possibly the species of the tropical New World may also prove to be generically distinct from the type species, *Agonostomus telfairii* Bennett, 1832, of Mauritius. If so, the New World species will take the generic name *Dajaus* Valenciennes *in* Cuvier and Valenciennes, 1836,[3] which has been used by Jordan, Evermann, and Clark (1930:254), Beltrán (1934:12), and de Buen (1947:281).

Distribution. Both coasts of tropical America, including the West Indies, from sea level to mountain streams. In the eastern Pacific, from Arroyo de Santa Cruz, Baja California (see records, infra), and Río Yaqui, Sonora, Mexico (Univ. Michigan Mus. Zool. No. 157267), to "central Panama" (Hildebrand, 1938:323); possibly to Río Condoto, a tributary of Río San Juan, Colombia; and perhaps to Río Dagua, Colombia. The record of *Agonostomus monticola* from Pacasmayo, Peru (Pearson, 1937:97), is erroneous; I have examined Pearson's specimens and have found them referable to *Mugil cephalus* Linnaeus.

According to Eigenmann (1922:187), the record of *Agonostomus nasutus* from Río Condoto, Colombia (Regan, 1914:33), may be referable to *Joturus daguae* Eigenmann, 1917. However, I am impressed by the resemblance of *Joturus daguae* to *Agonostomus monticola* (cf. Eigenmann, 1917:682; 1922:187). If the two prove to be identical, the range of *Agonostomus monticola* will be known to extend southward to the Río Dagua, Colombia, the type locality of *Joturus daguae.*

Fresh-water status. Complementary. Typically in fresh water except when

[4] Because they considered this record doubtful, Gosline and Brock (1960) omitted *Agonostomus* from their handbook in which they included "an account of every native inshore fish that seems to have been validly recorded from Hawaiian waters" (William A. Gosline, personal communication).

breeding and except in early stages; running into streams when young; later descending to breed in the sea (Anderson, 1957:424).

Baja California fresh-water records. Arroyo de Santa Cruz, Sierra de las Cacachilas, south of La Paz (Vaillant, 1894:73, as *Neomugil digueti*). San José del Cabo (Rutter, 1896:263, as *Agonostomus nasutus*).

Gerridae—Mojarras

The fishes of this family inhabit the tropical seas (Jordan and Evermann, 1898:1366).

Eucinostomus gracilis (Gill, 1862)

Affinities. Closely related to *Eucinostomus argenteus* Baird and Girard, 1855, with which it has long been confused.

Distribution. Bahía Magdalena, Baja California (Calif. Acad. Sci. No. 21227), and Gulf of California (Evermann and Jenkins, 1891:159, as *Gerres gracilis*), to the Galápagos Islands (Boyd W. Walker, personal communication).

Fresh-water status. Sporadic. More commonly vagrant into fresh waters than other species of the genus (Carl L. Hubbs, personal communication).

Baja California fresh-water records. San José del Cabo (Rutter, 1896:264; Osburn and Nichols, 1916:164; as *Eucinostomus californiensis*). These records are referred to this species with some doubt, although a specimen in the Stanford Natural History Museum, No. 5077, labeled "*Eucinostomus californiensis*, San José del Cabo, Lower Calif., J. F. Abbott" definitely represents *Eucinostomus gracilis*.

Gerres cinereus (Walbaum, 1792)

Affinities. A Pacific representative of this species was described as *Gerres simillimus* Regan, 1907, and the two were regarded as geminate species (Regan, 1906–1908:xxxi, 38). No difference between Atlantic and Pacific material was detected by Meek and Hildebrand (1925:590).

Distribution. Both coasts of America. On the Pacific coast, from Bahía Santa María (vicinity of Cabo San Lázaro), Baja California (Boyd W. Walker, personal communication), and Gulf of California (Osburn and Nichols, 1916:165, as *Xystaema cinereum*), to Bahía Chimbote, Peru (Hildebrand, 1946:239).

Fresh-water status. Sporadic. Rather rare in fresh water (Carl L. Hubbs, personal communication).

Baja California fresh-water record. San José del Cabo (Osburn and Nichols, 1916: 165, as *Xystaema cinereum*).

Lutjanidae—Snappers

This family is widely distributed in tropical and warm seas (Berg, 1940:475).

Lutjanus novemfasciatus Gill, 1862

Affinities. Scarcely distinguishable from its geminate species, *Lutjanus cyanopterus* (Cuvier *in* Cuvier and Valenciennes, 1828),[3] of the Atlantic coast of tropical America (Jordan and Fesler, 1893:440). This geminate relationship was mentioned by Jordan (1908:76).

Distribution. Laguna Santa María, Lat. 24° 47′ N., Long. 112° 16′ W., Baja California (Stanford Natur. Hist. Mus. No. 48261), and Gulf of California (Evermann and Jenkins, 1891:146), to Indefatigable Island, Galápagos Islands (Calif. Acad. Sci. Nos. 2781–2784).

Fresh-water status. Sporadic, especially when young.

Baja California fresh-water record. San José del Cabo (Osburn and Nichols, 1916: 163, as *Neomaenis novemfasciatus*).

Lutjanus argentiventris (Peters, 1869)

Affinities. This snapper and *Lutjanus apodus* (Walbaum, 1792), of the Atlantic, have been regarded as geminate species (Jordan, 1908:76); the two are distinguishable largely by color, dentition, and

average gillraker counts (see Meek and Hildebrand, 1925:510–511, 513–514).

Distribution. Laguna Santa María, Lat. 24° 47′ N., Long. 112° 16′ W., Baja California (Calif. Acad. Sci. No. 21228), and Gulf of California (see record, infra), to Bahía Lobos de Afuera, Perú (Hildebrand, 1946:231).

Fresh-water status. Sporadic. This snapper, especially when young, enters fresh water (cf. Gunter, 1957:13).

Baja California fresh-water record. Reported taken in fresh water in the laguna at the mouth of Arroyo Mulegé (Boyd W. Walker, personal communication).

Haemulidae—Grunts

These fishes inhabit the warm seas (Jordan and Evermann, 1898:1290).

Pomadasys bayanus Jordan and Evermann, 1898

Affinities. This species [5] and *Pomadasys crocro* (Cuvier *in* Cuvier and Valenciennes, 1830),[5] of the Atlantic, have been regarded as geminate species (Regan, 1906–1908:xxxi). They have been said to differ in squamation, size of mouth, and depth of body (Meek and Hildebrand, 1925:558). The question of their relationship may be a close one; the two have been said to be closely related, and (in the same paper) to be probably not distinct (Hildebrand, 1939:20, 28, 32).

Distribution. San José del Cabo, Baja California (Gilbert and Starks, 1904:109), to Bahía Santa Elena, Ecuador (Boulenger, 1899:3, as *Pristipoma labraciforme*).

Fresh-water status. Vicarious.

Baja California fresh-water record. San José del Cabo (Gilbert and Starks, 1904: 109). Although it was stated that "The records do not show whether this specimen was taken in the river at San José, or in the sea," the species is included in this paper because of general statements, as by Jordan and Evermann (1898:1331), that it is probably confined to fresh water.

Sciaenidae—Croakers

This varied family, consisting principally of marine shore fishes, is widely distributed in tropical and temperate waters, being particularly well represented in the Panamic fauna (Hubbs and Lagler, 1958: 116).

Micropogon megalops Gilbert, 1890

Affinities. Apparently not very closely related to any congener. The several congeneric species, all of which are American, are about equally divided between the Atlantic and the Pacific coasts, and are largely restricted to tropical or subtropical shores. (See Jordan and Evermann, 1898:1461–1464.)

Distribution. Recorded only from the Gulf of California (Fowler, 1944:510).

Fresh-water status. Sporadic.

Baja California fresh-water record. Reported as occasionally entering fresh water in the mouth of the Colorado River (Boyd W. Walker, personal communication).

Cynoscion xanthulus Jordan and Gilbert, 1882

Affinities. This species is close to *Cynoscion albus* (Günther, 1864); it does not appear to be the Pacific representative of any Atlantic American species (cf. Jordan and Evermann, 1898:1402, 1411).

Distribution. Head of Gulf of California, southward at least to Mazatlán, Sinaloa, Mexico (Walford, 1937:138). Its occurrence in Salton Sea, California, represents a recent introduction by man (Douglas, 1953:265).

Fresh-water status. Sporadic.

Baja California fresh-water record. Reported as occasionally entering fresh water in the mouth of the Colorado River (Boyd W. Walker, personal communication).

[5] *Pomadasys branickii* (Steindachner, 1879) and *Pomadasys crocro* have also been regarded as geminate species (Jordan, 1908:76).

Cynoscion macdonaldi Gilbert, 1890

Affinities. This species, called "totuava" by Gilbert (1890:65), Chute (1928:275), Walford (1937:132), and others, and "totoaba" by Beltrán (1934:12) and Berdegué (1956:235), does not appear to be closely related to any other North American sciaenid (Boyd W. Walker, personal communication).

Distribution. Head of Gulf of California, southward at least to Río Fuerte, Sinaloa, Mexico (Gilbert, 1890:65).

Fresh-water status. Sporadic, with approach toward diadromy. Regarded as typically anadromous by Berdegué (1956: 235), but its spawning migrations usually take it only into brackish water.

Baja California fresh-water record. Reported as occasionally entering fresh water in the mouth of the Colorado River (Boyd W. Walker, personal communication).

Cottidae—Sculpins

Numerous species of this family occur in the North Pacific, smaller numbers in the Arctic Ocean and in the North Atlantic, and a very few in the Antarctic (Hubbs and Lagler, 1958:116).

Leptocottus armatus australis Hubbs, 1921

Affinities. This is the southern representative (distinguished by fewer rays in the vertical fins) of a species that extends northward to Alaska (Hubbs, 1921:2). The genus *Leptocottus* is monotypic (Bolin, 1944:96).

Distribution. Morro Bay, California (Hubbs, 1921:5), to Bahía San Quintín, Baja California (Bolin, 1944:98, as *Leptocottus armatus*).

Fresh-water status. Sporadic.

Baja California fresh-water records. ". . . a shallow stream emptying into the ocean at Rosario [= Rosarito], about 15 miles below the boundary line and near the Coronado Islands" (Smith, 1883:235, as *Leptocottus armatus*). Arroyo San Miguel, one-half mile from ocean (Univ. Michigan Mus. Zool. No. 129588).

Gasterosteidae—Sticklebacks

The fishes of this family are confined to the northern hemisphere (Meek, 1916: 187, Fig. 68).

Gasterosteus aculeatus microcephalus Girard, 1854

Affinities. This partly plated, fluviatile stickleback has been regarded as a distinct species (Eigenmann, 1886:245), as a subspecies (Jordan and Hubbs, 1925:202), and as a doubtfully recognizable form (Myers, 1930:101). It is intermediate between the fully plated *Gasterosteus aculeatus aculeatus* Linnaeus, 1758, generally of marine habitat, and the plateless *Gasterosteus aculeatus williamsoni* Girard, 1854, of the Santa Ana system of streams in southern California (Jordan and Hubbs, 1925:200–202; cf. Culver and Hubbs, 1917:83).

Distribution. Bering Strait, Alaska (Eigenmann, 1886:246), to Arroyo del Rosario, Baja California (Carl L. Hubbs, personal communication).

Fresh-water status. Vicarious, especially in the southern part of its range, where this subspecies is almost wholly confined to fresh water.

Baja California fresh-water records. "Tia Juana Hot Springs, about 3 miles below the boundary line . . . also . . . Wild Cat Cañon, a few miles farther south" (Smith, 1883:233). "Wildcat Cañon, a tributary of the Tia Juana River" (Eigenmann. 1892:144). Arroyo Médano, Arroyo Santo Tomás, Arroyo San Vicente (Arroyo San Isidro), Arroyo San Rafael (Arroyo Seco) near Cabo Colnett, and Arroyo del Rosario (Carl L. Hubbs, personal communication).

Syngnathidae—Pipefishes

The fishes of this family are found in all warm seas (Jordan and Evermann, 1896: 760).

Pseudophallus starksii (Jordan and Culver, 1895)

Affinities. The only known congeners of this American fresh-water pipefish are *Pseudophallus elcapitanensis* (Meek and Hildebrand, 1914), of the Pacific coast, and *Pseudophallus mindii* (Meek and Hildebrand, 1923), of the Atlantic coast (Herald, 1959:473).

Distribution. San José del Cabo, Baja California (Rutter, 1896:263, as *Siphostoma starksi*), to Santa Rosa, Ecuador (Starks, 1906:783, as *Syngnathus starksi*).

Fresh-water status. Vicarious.

Baja California record. San José del Cabo (Rutter, 1896:263, as *Siphostoma starksi*).

Eleotridae—Sleepers

These fishes are largely tropical and subtropical in distribution (Berg, 1940: 487).

Gobiomorus maculatus (Günther, 1859)

Affinities. Closely related to *Gobiomorus dormitor* Lacépède, 1798,[6] of the Atlantic slope of America (Meek and Hildebrand, 1916:353; Hildebrand, 1938:340), and less closely to *Gobiomorus polylepis* Ginsburg, 1953, of Pacific coastal streams of México (Miller, 1959:9).

Distribution. Cabo San Lucas, Baja California (Gill, 1860:124, as *Philypnus lateralis*), and Río Yaqui, Sonora, México (Miller, 1959:5), to Etén, Peru (Starks, 1906:799, as *Philypnus lateralis*).

[6] *Gobiomorus maculatus* and *Gobiomorus dormitor* apparently evolved from a common ancestral stock. *Gobiomorus polylepis* may have been derived from *Gobiomorus dormitor;* it has been suggested that the differentiation of *Gobiomorus polylepis* may have been associated with a seaway (postulated by Mayr, 1946:Fig. 1) extending across the Isthmus of Tehuantepec from late Miocene to middle Pliocene time (Miller, 1959:9). Evidence published by Durham, Arellano, and Peck (1955), however, indicates that there was no seaway across the Isthmus of Tehuantepec during the Cenozoic.

Fresh-water status. Complementary.

Baja California fresh-water records. San José del Cabo (Rutter, 1896:264; Osburn and Nichols, 1916:175; as *Philypnus lateralis*).

Dormitator latifrons (Richardson, 1844)

Affinities. Distinguished by its higher gillraker count from its geminate species, *Dormitator maculatus* (Bloch, 1790), of the American Atlantic coast and rivers (Meek and Hildebrand, 1916:356). A subspecies, *Dormitator latifrons mexicanus* Ginsburg (1953:20), said to be restricted to the Pacific coast of México, has been distinguished from the typical subspecies, *Dormitator latifrons latifrons* (Richardson), of the Pacific coast of Central America.

Distribution. Punta Lobos two miles southwest of Todos Santos, Baja California (Calif. Acad. Sci. No. 21231), and Río Yaqui, Sonora, México (Branson, McCoy, and Sisk, 1960:220), to Guayaquil, Ecuador (Günther, 1861:112, as *Eleotris maculata*).

Fresh-water status. Complementary.

Baja California fresh-water records. Mulegé, upper part of town, fresh-water stream above tide level (Calif. Acad. Sci. No. 21229). Arroyo San José, San José del Cabo (Rutter, 1896:265, as *Dormitator maculatus*). San José del Cabo (Wales, 1932:168, as *Dormitator maculatus;* in fresh water, fide Ira L. Wiggins, personal communication). San José del Cabo and Bahía Agua Verde (Osburn and Nichols, 1916: 175, as *Dormitator maculatus*). La Playa, east of San José del Cabo (Calif. Acad. Sci. No. 21230).

Eleotris picta Kner and Steindachner, 1863

Affinities. Distinguishable by squamation and color from its geminate species, *Eleotris pisonis* (Gmelin, 1788), of the American Atlantic coast (see Hildebrand, 1938:347–348).

Distribution. Colorado River near Winterhaven, California (Hubbs, 1953a:69), to Guayaquil, Ecuador (Starks, 1906:799).

Fresh-water status. Complementary.

Baja California fresh-water records. San José del Cabo (Jordan and Gilbert, 1882b: 380, as *Culius aequidens;* Rutter, 1896:265; Osburn and Nichols, 1916:175). In view of the tropical distribution of this species, the specimen recorded from near Winterhaven, Imperial County, California (Hubbs, 1953a:69), must have passed through fresh water in Baja California in order to reach that locality.

Gobiidae—Gobies

This family inhabits all warm seas, some of its representatives occurring in rivers (Berg, 1940:487).

Awaous transandeanus (Günther, 1861)

Affinities. This goby differs slightly in several respects from its geminate species, *Awaous taiasica* (Lichtenstein, 1822), of the American Atlantic slope (Meek and Hildebrand, 1916:369; Hildebrand, 1938: 357). I follow Ginsburg (1933:21) in retaining the generic name *Awaous* Valenciennes *in* Cuvier and Valenciennes, 1837.[8]

Distribution. Cabo San Lucas, Baja California (Jordan and Gilbert, 1882a:368, as *Gobius banana*), and Río Yaqui, Sonora, Mexico (Univ. Michigan Mus. Zool. No. 157268), to Río Chanchan, near Guayaquil, Ecuador (Eigenmann, 1922:216); erroneously recorded by Regan (1906–1908:12, as *Chonophorus banana*) from southern California.

Fresh-water status. Complementary.

Baja California fresh-water records. San José del Cabo (Jordan and Gilbert, 1882b: 380, as *Gobius banana;* Jordan, 1895:494, as *Awaous tajasica;* Rutter, 1896:265, and Osburn and Nichols, 1916:175, as *Awaous taiasica*). La Purísima (Evermann, 1908: 29, as *Awaous taiasica*). "Pozas 'Boca de la Sierra,' en Municipio de Santiago del Territorio Sur" (de Buen, 1942:53, as *Chonophorus banana*).

Gillichthys mirabilis Cooper, 1864

Affinities. The unpublished investigations of George W. Barlow indicate that *Gillichthys detrusus* Gilbert and Scofield, 1898, is referable to the synonymy of *Gillichthys mirabilis.* The genus *Gillichthys* Cooper, 1864, has been treated as a subgenus of *Lepidogobius* Gill, 1859, by Ginsburg (1938:119).

Distribution. Tomales Bay, California (Roedel, 1953:143, to Guaymas, Sonora, México (Evermann and Jenkins, 1891: 162). This is essentially a Californian species, occurring disjunctly in the Gulf of California. In several faunal lists, this species has been said to occur as far north as Puget Sound (Jordan and Gilbert, 1881: 455; Eigenmann and Eigenmann, 1892: 354; Jordan and Starks, 1895:839; Kincaid, 1919:40; Schultz and DeLacy, 1936:138; Schultz, 1936:191). Reasons for doubting that this species ranges so far north have been published by Clemens and Wilby (1946:167). The occurrence of this species in Salton Sea, California, presumably represents an introduction by man (see Douglas, 1953:265).

Fresh-water status. Sporadic.

Baja California fresh-water records. Horseshoe Bend, near the mouth of the Colorado River, in Mexico (Gilbert and Scofield, 1898:499, as *Gillichthys detrusus*). Río Hardy: just above Pongo de Abajo; one mile down from tide gauge (Carl L. Hubbs, personal communication).

Species of Possible Occurrence in Fresh Water in Baja California

The following species were recorded from the mouth of Arroyo Mulegé without a specific statement that the water at the place of capture was fresh:

Clupeidae

Lile stolifera (Jordan and Gilbert, 1881)

"Mouth of Mulege River" (Osburn and Nichols, 1916:150, as *Sardinella stolifera*).

Gerridae

Eugerres peruvianus (Cuvier *in* Cuvier and Valenciennes, 1830)[3]

"Mulege, at mouth of river" (Osburn and Nichols, 1916:165, as *Gerres peruvianus*).

Carangidae

Oligoplites saurus (Bloch and Schneider, 1801)

"Mouth of Mulege River" (Osburn and Nichols, 1916:159).

Lutjanidae

Lutjanus colorado Jordan and Gilbert 1881

"Mulege, at the mouth of the river" (Osburn and Nichols, 1916:163, as *Neomaenis colorado*).

Haemulidae

Brachydeuterus leuciscus (Günther, 1864)

"Mulege at mouth of river" (Osburn and Nichols, 1916:164).

Sciaenidae

Umbrina sp.

"Mulege River at its mouth" (Osburn and Nichols, 1916:168, as *Umbrina xanti*); this record is based on an undescribed species (Carl L. Hubbs, personal communication).

That the following species may possibly have occurred in fresh water in Baja California is suggested by the records indicated:

Catostomidae

Catostomus latipinnis Baird and Girard, 1853

Suckers doubtfully referred to this species were recorded as abundant in Salton Sea during 1913 (Dawson, 1923:1948). To reach that locality, this Colorado River species would have had to pass through fresh water in Baja California. The identification was queried by Dawson (1923: 1948) and was rendered even more doubtful by his statement that the suckers in question "would weigh from five to fifteen pounds."

Cyprinidae

Plagopterus argentissimus Cope, 1874

"A few specimens were procured in the mouth of the Rio Gila at Yuma [Arizona]" (Gilbert and Scofield, 1898:496). This locality is so close to the international boundary as to suggest the possibility that under primitive conditions this minnow was carried downstream into Baja California during heavy floods.

Gerridae

Eucinostomus argenteus Baird and Girard, 1855

Since this species and *Eucinostomus gracilis* frequently occur together (Carl L. Hubbs, personal communication), it seems possible that it was represented among the specimens recorded as *Eucinostomus californiensis* from San José del Cabo by Osburn and Nichols (1916:164).

Erroneous Records

The following species have been erroneously recorded from Baja California:

Cyprinodontidae

Fundulus vinctus Jordan and Gilbert, 1882

Said to have been collected at Cabo San Lucas (Jordan and Gilbert, 1882a:355). Apparently based on material of the common Atlantic-coast species *Fundulus heteroclitus* (Linnaeus, 1766) "that had somehow become mixed with the Xántus collection" (Miller and Hubbs, 1954:234).

Fundulus extensus Jordan and Gilbert, 1882

Said to have been collected at Cabo San Lucas (Jordan and Gilbert, 1882a:355).

Apparently based on material of the common Atlantic-coast species *Fundulus diaphanus* (LeSueur, 1817) "that had somehow become mixed with the Xántus collection" (Miller and Hubbs, 1954:234).

Goodeidae

Ilyodon furcidens (Jordan and Gilbert, 1882)

The type material of *Characodon furcidens*, which was said to have been collected at Cabo San Lucas (Jordan and Gilbert, 1882a:354), was "very probably collected by Xántus in the state of Colima on the Mexican mainland" (Miller and Hubbs, 1954:234).

Introduced Species

The following introduced species have been reported from Baja California at the localities indicated.

Cyprinidae

Cyprinus carpio Linnaeus, 1758

A laguna of Salton River[2] at Seven Wells (south of monument No. 213, M.B.L.), about four miles south of the United States border, April 13 and 15, 1894; Gardner's Laguna, Salton River (south of monument No. 216, M.B.L.), April 22, 1894 (Edgar A. Mearns, unpublished field notes, as "carp"). Distributaries of the Colorado River: two miles above Pongo de Abajo; at junction of Hardy and Colorado rivers; just above Pongo de Abajo; 15 miles (by slough and river) south of El Mayor; five miles below Pongo de Abajo; one mile down from tide gauge—about 25 miles (by river) above mouth (Carl L. Hubbs, personal communication).

Gila orcuttii (Eigenmann and Eigenmann, 1890)

Introduced experimentally into Arroyo Santo Tomás (Carl L. Hubbs, personal communication).

Siphateles mohavensis Snyder, 1918

Introduced experimentally into Arroyo Santo Tomás (Carl L. Hubbs, personal communication).

Notropis lutrensis (Baird and Girard, 1853)

Distributaries of the Colorado River: two miles south of Gadsden, Yuma County, Arizona; two miles north of San Luis, Sonora; and 15 miles (by the Río Hardy slough and the river) below El Mayor (Hubbs, 1954:289).

Ictaluridae

Ictalurus punctatus punctatus (Rafinesque, 1818)

Río Hardy at El Mayor (J. Bruce Kimsey, personal communication).

Poeciliidae

Gambusia affinis affinis (Baird and Girard, 1853)

Arroyo San José, where this fish was introduced April 26, 1931 (Miller and Hubbs, 1954:234); Tijuana River two miles east of Tijuana; stream entering southwest corner of Valle de Santa Rosa 20 miles south of Ensenada; Arroyo San Miguel three miles east of highway; Laguna Santa María (San Simón) south of Bahía San Quintín; arroyo at Santiago, Cape District (about 23°28′ N., 109°43′ W.); San José del Cabo (water from Arroyo San José); distributaries of the Colorado River: Río Hardy at Meganito (2.1 miles north of El Mayor); four miles below junction of Río Hardy; just above Pongo de Abajo; 15 miles (by slough and river) south of El Mayor; one mile down from tide gauge—about 25 miles (by river) above mouth (Carl L. Hubbs, personal communication).

Centrarchidae

Micropterus salmoides salmoides (Lacépède, 1802)

Tijuana River two miles east of Tijuana; Laguna San Simón near Bahía San Quintín; distributaries of the Colorado River: Río Hardy at Meganito (2.1 miles north of El Mayor); one mile south of El Mayor; four miles below junction of Río Hardy (Carl L. Hubbs, personal communication).

Lepomis cyanellus Rafinesque, 1819

Tijuana River two miles east of Tijuana; stream entering southwest corner of Valle de Santa Rosa 20 miles south of Ensenada; Arroyo San Miguel; distributary of the Colorado River 15 miles (by slough and river) south of El Mayor (Carl L. Hubbs, personal communication).

Lepomis macrochirus macrochirus Rafinesque, 1819

Distributaries of the Colorado River: two miles south of Gadsden, Yuma County, Arizona; junction of Hardy and Colorado rivers; 15 miles (by slough and river) south of El Mayor (Carl L. Hubbs, personal communication).

Pomoxis annularis Rafinesque, 1818

Slough entering Colorado River about nine miles south of Morelos Dam (Robert R. Miller, in litt.). Four miles below junction of Hardy and Colorado rivers (Carl L. Hubbs, personal communication).

Pomoxis nigromaculatus (LeSueur, 1829)

Slough entering Colorado River about nine miles south of Morelos Dam (Robert R. Miller, in litt.). Distributary of Colorado River five miles below Pongo de Abajo (Carl L. Hubbs, personal communication).

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